

Factors affecting the nesting success of Swainson's thrush (*Catharus ustulatus*) along an elevational gradient

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Abstract

Montane birds experience a range of challenges that may limit their breeding success, including nest predation and severe climatic conditions. The continuing effects of climate change are causing shifts in biotic and abiotic factors that may compound these threats to montane bird species. In northeastern montane forests, many bird species are shifting downslope, potentially as the result of increased precipitation and temperature at higher elevations. Although lower elevations might be more favorable in terms of climatic conditions, nest predation is higher at lower elevations. Thus, montane birds might be faced with the opposing pressures of adverse climatic conditions at higher elevations and increased predation at lower elevations. We monitored nests of Swainson's thrush (*Catharus ustulatus*) along an elevation gradient in the White Mountain National Forest in New Hampshire in 2016, 2018, 2019 and 2021 to examine the effect of biotic and abiotic factors on nest survival. We found a significant negative effect of rain intensity (millimeters per hour per day) on daily nest survival, suggesting that heavier rain per hour decreases Swainson's thrush daily nest survival. Moreover, we found a negative interaction effect of elevation in conjunction with minimum daily temperature and average daily temperature, suggesting that at higher elevations, temperature, specifically on colder days, decreases Swainson's thrush nest survival. Our results provide evidence for a potential mechanism of how climate change will affect nesting survival of montane breeding birds as heavier precipitation events become more frequent and intense, a likely outcome due to the changing climate within the White Mountains and other montane ecosystems, putting other passerine species at risk in this system.

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Abstract

Montane birds experience a range of challenges that may limit their breeding success, including nest predation and severe climactic conditions. The continuing effects of climate change are causing shifts in biotic and abiotic factors that may compound these threats to montane bird species. In northeastern montane forests, many bird species are shifting downslope, potentially as the result of increased precipitation and temperature at higher elevations. Although lower elevations might be more favorable in terms of climactic conditions, nest predation is higher at lower elevations. Thus, montane birds might be faced with the opposing pressures of adverse climactic conditions at higher elevations and increased predation at lower elevations. We monitored nests of Swainson’s thrush (*Catharus ustulatus*) along an elevation gradient in the White Mountain National Forest in New Hampshire in 2016, 2018, 2019 and 2021 to examine the effect of biotic and abiotic factors on nest survival. We found a significant negative effect of rain intensity (millimeters per hour per day) on daily nest survival, suggesting that heavier rain per hour decreases Swainson’s thrush daily nest survival. Moreover, we found a negative interaction effect of elevation in conjunction with minimum daily temperature and average daily temperature, suggesting that at higher elevations, temperature, specifically on colder days, decreases Swainson’s thrush nest survival. Our results provide evidence for a potential mechanism of how climate change will affect nesting survival of montane breeding birds as heavier precipitation events become more frequent and intense, a likely outcome due to the changing climate within the White Mountains and other montane ecosystems, putting other passerine species at risk in this system.

Keywords: montane, nest survival, abiotic factors, White Mountains

Introduction

Montane bird species that breed within high elevation forests are particularly vulnerable to the effects of climate change due to the narrow elevational ranges they inhabit (Scridel et al., 2018), making them susceptible to extirpation (Sekercioglu et al., 2008) if their elevational ranges are compressed due to climate change and anthropogenic land uses (Rodenhause et al., 2008). Research within northeastern forests of the United States confirms that the average temperature within this system has increased over the last several decades (Murray et al., 2021; Wason et al., 2017), which is likely causing recently documented downslope shifts in montane birds (DeLuca & King, 2017) and high-elevation vegetation (Foster & D’Amato, 2015; Wason et al., 2017).

Coincident with these changes, the elevational distribution of montane birds has also shifted downwards (DeLuca & King, 2017), although the motives for these shifts, and their consequences for montane breeding birds, is unclear. Within northeastern high elevation forests, populations of montane birds are declining (Ralston et al., 2015), potentially because elevational range shifts are exposing birds to unfamiliar resources and conditions along the elevation gradient that could affect their breeding success. For example, breeding success of blackpoll warblers (*Setophaga striata*), is lower at low elevations, likely due to increased abundance of red-squirrels, a major nest predator in this system (DeLuca, 2013). Similarly, dark-eyed juncos (*Junco hyemalis*) at high elevations produced nestlings in better condition and experienced higher survival rates than birds at lower elevations (Bears et al., 2009). These examples raise the possibility that lower elevations are less suitable for montane birds, and that the documented downward shifts in their elevational ranges may expose these species to elevated nest predation (Boyle 2008, Camfield et al., 2010; DeLuca, 2013).

Alternatively, abiotic factors, such as cold temperatures and increased precipitation, may affect reproductive success of birds nesting at high elevations (Pierce et al., 2019). Warmer temperatures promote larger egg size (Johnson 2000; Lessells et al., 2002), increased clutch size (Hargrove & Rotenberry, 2011; Rotenberry & Wiens, 1991), and improved hatching and fledgling success (Martin, 1987; Reid et al., 2000), and greater food availability (Bears et al., 2009; Svensson & Nilsson, 1995). Increased precipitation may also negatively influence nesting survival of breeding birds (Bordjan & Tome, 2014; Dinsmore et al., 2002; Dreitz et al., 2012; Fisher et al., 2015; McCain & Colwell, 2011; Öberg et al., 2015; Schöll & Hille, 2020), particularly during intense rain events (Öberg et al., 2015; Sexson & Farley, 2012). High elevation sites in the Northeast U.S. are experiencing more frequent rain events (Wright 2009; Karmalkar & Bradley, 2017). Precipitation is known to negatively affect avian nesting success and as precipitation intensities are increasing in frequency,

this raises concern for montane birds nesting in this region.

Due to the reported vulnerability of montane birds and the threats that a changing climate imposes on high elevation species (Ralston & DeLuca, 2020; Ralston & Kirchman, 2013), we located and monitored nests of a representative montane bird species, the Swainson's Thrush (*Catharus ustulatus*) within the White Mountains of New Hampshire, USA. We considered three predictions: 1) nests at higher elevations would be more likely to be successful due to lower predation events (Boyle, 2008; Camfield et al., 2010), 2) average minimum daily temperature, minimum daily temperature, or higher temperature range (i.e., greater daily variability in temperature) would negatively affect daily survival rate (Pierce et al., 2019), and 3) increased daily cumulative precipitation, more intense rain bouts (i.e., more millimeters of rain per hour), or heavy precipitation events would negatively affect daily survival rate (Dinsmore et al., 2002; Dreitz et al., 2012; Pierce et al., 2019). Documenting the abiotic effects on reproductive success of birds along elevation gradients will contribute to a better understanding of future climatic responses by species (Martin, 2001; Tingley et al., 2012), something that is largely understudied within northeastern montane forests.

Materials and Methods

Study area and study species.

We researched nest survival of Swainson's thrush along an elevational gradient in the White Mountains of New Hampshire, USA at Mt. Jefferson (approximately 500-1,250m; 44.3045° N, 71.3176° W) and Bartlett Experimental Forest (hereafter referred to as BEF; approximately 200-300m; 44.0556° N, 71.2973° W). The Swainson's Thrush is a Nearctic Neotropical migratory songbird which is moderately common and breeds along a wide elevation gradient within this system (Figure 1, 200-1,250m; Mack & Yong, 2020). Though their populations were once documented to be declining (Holmes & Sherry, 2001; Robbins et al., 1989), recent research has shown their ranges to be increasing (Ralston et al. 2015) as well as shifting downslope (DeLuca and King, 2017), suggesting population increases. Nest survival data were collected from May through August 2016, 2018, 2019, and 2021 (field season canceled in 2020 due to COVID-19) in the White Mountains at Mt. Jefferson (all years) and BEF (2018, 2019, and 2021). The surrounding plant community on Mt. Jefferson below 700m in elevation consists of northern hardwood forest dominated by American beech (*Fagus grandifolia*), paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*). Between 700m and 1,300m is a mixed forest of deciduous and coniferous of birch trees and red spruce (*Picea rubens*), balsam fir (*Abies balsamea*). As elevation increases above 1,250m, high alpine boreal tree species become more abundant before reaching treeline at ~1,350m. BEF ranges from 200-400m in elevation, though to capture low elevation breeding populations of Swainson's thrush, nests were searched only between 200-300m. Tree species within BEF are primarily American beech, paper birch, red spruce and eastern hemlock (*Tsuga canadensis*), though Swainson's thrush typically build their nests in dense patches of small (<8 cm DBH) red spruce and eastern hemlock trees.

Swainson's thrush typically arrive in New Hampshire between late May to early June and their nesting period is 28 days (+/- 2) with four stages: nest building (4 days), laying and incubation of the eggs (12 days), and provisioning and caring for nestlings before fledging (12 days). Female Swainson's thrush typically have one brood, though they can reneest, and they build their nest in red spruce, balsam fir, and paper birch trees, ranging anywhere from 3-10m in height (Mack and Yong, 2020). Nests are typically built with bark from yellow birch or paper birch, as well as miscellaneous tree branches, twigs, and moss, and can occasionally have artificial materials in them (i.e., plastic bags, bottle caps).

Nest monitoring.

Fieldwork to locate breeding pairs and nests began approximately 25 May (+/- 2) each year. Parental behavioral cues and rigorous nest searching are both important techniques to find nest locations (Martin and Geupel, 1993). Searching effort was relatively evenly distributed among sites. Once found, nests were marked with a GPS and flagged no less than 8m away from the active nest so as not to disturb the nesting pair. We monitored each nest every 2-3 days until they were close to fledging (~11 days old), and then

every day after until fledged. If presumed fledged, we searched the area meticulously to take notes such as provisioning behavior from parents (i.e., food in their bill, alarm calling, etc.) or visual sightings. A successful nest yielded at least one fledged bird, and a failed nest was depredated or abandoned. Nests were considered depredated if an active nest was observed with cracked or missing eggs, dead young nestlings (<11 days old) and/or adults, or a nest that was pulled apart. On occasion, nests were abandoned and confirmed as such if adults were absent for [?]3 visits. We collected nesting data including initiation date (i.e., date the first egg was laid), clutch size, hatch date (i.e., date the first egg hatched), and nestling condition (i.e., how old the nestlings were at the date checked and what their appearance was). When hatch date was unknown, we back-calculated nest age based on the nestlings' condition. Finally, if nest initiation date was unknown, we backdated from known or estimated hatch date, assuming one egg was laid per day, incubation occurred for 12 days, and nestlings were at least 11 days old before fledgling (Halupka *et al.*, 2018). Nests were binned in four groups ("BEF" = 200-300m; "Low Jeff" = 500-700m; "Mid Jeff" = 701-900m; "High Jeff" = 901-1,250m) to correspond with the matching spatial precipitation and temperature data that was collected along the elevation gradients.

Environmental covariates.

Hourly ambient temperature (°C) was collected using Thermocron ® iButton loggers (Maxim Integrated) from 25 May to 31 July 2016, 2018, and 18 May-3 August 2019 and 2021. Loggers were placed at long-term GPS coordinates (Duclos *et al.*, 2019) that represented the elevation gradient we were interested in and corresponded with bins used for nests (280m, "BEF"; 550m, "Low Jeff"; 800m, "Mid Jeff"; and 1,200m, "High Jeff"). Loggers were held in a Holden shield to protect the iButton from direct solar exposure (Holden *et al.*, 2013). Daily average temperature, minimum daily temperature, and temperature range was calculated and used to analyze the effect on daily nest survival. Precipitation data were collected in 2019 and 2021 using Onset ® HOBO ® RG3-M rain gauges. To capture the daily cumulative rainfall across the elevation gradient, we placed three rain gauges at Mt. Jefferson at locations similar to the iButton loggers (500m, "Low Jeff"; 800m, "Mid Jeff"; and 1,200m, "High Jeff") in open areas with no tree canopy. We used precipitation data collected in BEF (250m, "BEF") from the NSF National Ecological Observatory Network (NEON), an open-sourced data platform. Within each rain gauge is a tipping bucket that measured how much cumulative precipitation fell each day throughout the season. Precipitation data were not collected in 2016 and 2018 and, therefore, will not be analyzed with nest survival data from those years. Rain intensity was quantified by how much rain (mm) was recorded per hour per day.

Due to equipment malfunctions from the HOBO Rain Gauge placed at 500m (i.e., "low-Jeff"), precipitation data from 1 July – 3 August 2021 was lost. To estimate the missing daily precipitation at this location for the remainder of the 2021 season, we used the Random Forest (RF) machine-learning algorithm. When tested against other algorithms to estimate large amounts of missing precipitation data, the RF was the most preferred method (Aguilera *et al.*, 2020), in the context of our data. The RF algorithm is a non-parametric imputation method that takes observed values of each variable, and predicts the missing values, without having any assumptions about the distribution of data or imputation models. We followed the recommendations from Aguilla, Guardiola-Albert and Serrano-Hidalgo (2020) and included dummy variables to account for no rain days, a Hanssen-Kuipers (HK) score to distinguish between occurrences and non-occurrences of a rain event (Hanssen and Kuipers 1965), and an NRMSE (normalized root error mean squared error) error metric to allow for the comparison of the average relative differences between the observed and imputed missing values (Supplementary Figure 1).

Dummy variables were produced by randomly assigning the missing data matrix with presence (1) or absence (0) of rain days. For each day we considered the dates where the dummy variable was 0 and input 0 for that day, and only the days the dummy variable predicted a value of 1 did we input the numeric value estimated from the RF algorithm. The HK score ranges between -1 to +1, where 0 represents no skill or a random estimate, and 1 indicates a perfect estimate, and has been widely used to evaluate yes/no meteorological forecasts (Woodcock 1976, Teegavarapu 2014, Kim and Ryu 2016). We used the package *missForest* in R Studio (version 2022.07.0; R Core Team 2022) for the RF algorithm to input missing precipitation values.

Statistical analysis.

Daily survival rate. We measured the daily survival rate (DSR), i.e., the probability that a nest survives one day (Dinsmore et al., 2002; Mayfield, 1961) to better understand how abiotic factors (temperature and precipitation), nest initiation date, elevation, and other temporal variables influence nesting survival of Swainson’s thrush. We analyzed DSR using the RMark package (Laake et al., 2013) in R Studio (v. 2022.07.0). This package calculates estimates of DSR using a maximum likelihood estimator with the logit-link function with predictor variables. The assumptions are that DSR is the same for all nests on all days and for all nest ages (nest fates are independent and identically distributed: *iid* ; Rotella, 2006) though there is currently no goodness-of-fit test for nest survival models in rMark (Dinsmore et al., 2002; Laake et al., 2013), and rMark cannot run mixed models (Rotella et al., 2004). Daily survival probabilities were calculated by taking the beta parameter estimate and raising it to the power of the number of nesting days (i.e., 28 for Swainson’s thrush). See Rotella et al. (2004) for a more in-depth description of how MARK interprets the temporal covariates as an encounter history. We included nests in our analysis when they met the following criteria: 1) known day the nest was found, 2) the last day the nest was active, 3) the last day the nest was checked, and 4) known nest fate (i.e., fledged or failed). We standardized the ordinal dates to be the duration that nests were first active (i.e., initiation date) which translated to 0 (1 June) until the last known active nest date, 63 (2 August) over the four years (number of occupancy days, NOCC = 63).

Environmental covariates. We used cumulative daily precipitation (mm; 2019, 2021), categorical rain events denoted as either no rain (0), “light” rain (0.1-6.9mm) or “heavy” rain (>7mm), and rain intensity (mm per hour) as predictor variables in our daily survival models. Rain event parameters were determined by examining the data in a frequency plot and categorizing “light” and “heavy” rain days accordingly. Average daily temperature, minimum daily temperature, and daily temperature range (°C; 2019, 2021) were separately modeled against daily survival to better understand how temperature in the White Mountains affects daily survival probability. Nests from 2016 and 2018 were excluded from precipitation and temperature analysis because we did not collect climate data from those years. Nests were binned in four groups (“BEF” = 200-300m; “Low Jeff” = 500-700m; “Mid Jeff” = 701-900m; “High Jeff” = 901-1,250m) to correspond with the matching spatial precipitation and temperature data that was collected along the elevation gradients.

Model selection. We began the model building stage by testing pairwise correlation comparisons in our predictor variables for our nest survival data (elevation, nest age, initiation date) and the environmental covariates (elevation, daily average temperature, minimum daily temperature, temperature range, daily cumulative precipitation, and rain intensity). This comparison revealed a negative correlation coefficient with elevation and daily temperature range ($p = -0.46$) and, therefore, these variables were not included in the same model.

We created 14 *a priori* DSR univariate models that examined the effects of temporal variables including nest age, julian date, and year, as well as initiation date, elevation, and our weather covariates on the daily nest survival of Swainson’s thrush (Table 1; models 2-3, 5-13). We also included an intercept model (model 1) in which only daily survival rate was estimated, and a quadratic time trend (model 4), which allows for nest survival to fit a curvilinear pattern, since survival over time is not always linear. We included several other models (Supplementary Table 1) in the initial stages of model building to test for any relevant additive or interaction effects, including a global model, but because they did not perform well, they were removed from our final analysis.

After evaluating variables *a priori* models above, and removing necessary models that performed poorly, we added two additional models with interaction effects (year and elevation) with seasonal time. This predictor variable performed the best against DSR (Table 1; models 15 and 16). We then built four more models that included biological interaction and additive effects we were interested in (models 17-23) to explore all potentially important relationships between our variables and DSR. In the final stage of model building, we used AIC (Akaike’s Information Criterion) to find support for the most parsimonious model that best described DSR (Anderson & Burnham, 2002) and compared models 1-5 (Table 1) between all years, and models 6, 8-13, and 19-20 for 2019 and 2021 (Table 1). We considered the best model to have a $[\Delta]AIC_c$ value of zero, variables in models that were within 4 $[\Delta]AIC_c$ of the best model with 95% confidence intervals not

including zero to be strongly supported (Arnold, 2010), and variables in models within 4 Δ AICc with 90% confidence intervals to have some support (Hein et al., 2008; Long et al., 2008). Model outputs are reported with 95% confidence intervals otherwise noted.

Results

Data summary.

A total of 58 nests were found and included in the initial stage of analyses between 2016 ($n=5$), 2018 ($n=6$), 2019 ($n=21$), and 2021 ($n=26$) from 31 May to 2 August. Out of these 58 nests, 24 succeeded (42%) and 34 nests failed (58%), either due to nest predation (71%) or abandonment (29%). We found 10 nests at “BEF”, 14 nests at “Low Jeff”, 19 nests at “Mid Jeff”, and 15 nests at “High Jeff”. Mean daily temperature (Fig. 1A) and precipitation (Fig. 1B) varied depending on the year and elevation. Across both study sites throughout the season, average minimum daily temperature was 11.4degC ($se = 0.21$), and average temperature range was 11.5degC ($se = 0.25$). When we examined the effects of initiation date, precipitation, and temperature from 2019 and 2021, 44 nests were included in the analysis. After backdating for initiation and hatch date, we removed 3 nests from the analysis because nests were found in the incubation stage but failed before hatch date. Average initiation date was June 17th (± 2 days), and average clutch size was 3.1 eggs in 2019 and 3.2 in 2021. The RF algorithm calculated 34 missing days of precipitation data (NRMSE = 0.078, HK = 0.39) for the “Low Jeff” Rain Gauge (1 July – 3 August 2021).

Daily survival rate.

All years. The first round of model building included temporal variables with nests from all years (2016, 2018, 2019, 2021; NOCC=63; Table 2). Daily survival probability for Swainson’s thrush across the four-year sampling period was 23%. We did not find support that elevation affected daily survival probability ($b = -0.0005$, 95% CI [-0.0008, 0.0019], 90% CI [0.0017, -0.0005]). The model with the most support suggested that nests have a higher probability of failing as the season progresses (Table 2; $b = -0.02$, 95% CI [-0.05, 0.0092]). When we examined linear time within 90% confidence intervals, the model suggests some support ($b = -0.02$, 90% CI [-0.003, -0.051]). We examined all models using AIC and found two models that were within 2 Δ AICc values of one another and demonstrated the strongest support above the null model, which were the quadratic time trend and linear time trend (Table 3). Finally, we ran an interaction effect between time and elevation ($b = -0.00004$, 95% CI [-0.0001, 0.00006]) but this model did not perform well and was removed from our model comparison output.

2019 and 2021. In the second stage of our analysis, we built models for nests from 2019 and 2021 (Table 2) and included temperature and precipitation covariates, as well as effects with initiation date against daily survival rate. There was no evidence that nest survival was affected by either initiation date ($b = -0.007$, 95% CI [-0.047, 0.032]) or elevation ($b = 0.0003$, 95% CI [-0.0009, 0.0016]). Nest survival was negatively related to linear time ($b = -0.03$, 90% CI [-0.002, -0.057]), indicating some support that nest survival declined over the 2019 and 2021 nesting season.

We ran an interaction effect between elevation and several other meaningful parameters, including initiation date ($b = -0.00003$, 95% CI [-0.0001, 0.00008]), linear time ($b = -0.00003$, 95% CI [-0.0003, 0.00006]) and nest age ($b = 0.00004$, 95% CI [-0.00008, 0.00016]) but we did not find support for these relationships. We also included an interaction between linear time and year (Table 1, model 15) because precipitation varied markedly among years (Fig. 1A&B), and we were interested in evaluating year for other interannual variation, but this relationship did not demonstrate an effect (Table 2; $b = -0.002$, 95% CI [-0.07, 0.06]).

Environmental covariates (2019 and 2021 only). Our models did not show support that average daily temperature ($b = -0.02$, 95% CI [-0.15, 0.11]), minimum daily temperature ($b = -0.02$, 95% CI [-0.13, 0.08]) or daily temperature range ($b = 0.06$, 95% CI [-0.04, 0.16]) affected daily nest survival in Swainson’s thrush (Table 2). We found strong support that an interaction between elevation and minimum daily temperature affected daily survival rate ($b = -0.007$, 95% CI [-0.001, -0.0002]). We also found strong support for an inter-

action between elevation and average daily temperature ($b = -0.0006$, 95% CI [-0.001, -0.000009]). Because our other temperature variable (i.e., daily temperature range) demonstrated collinearity with elevation, we did not test interaction effects of these relationships.

We examined “light” and “heavy” rain events and found support that light rain (i.e., 0-6.9mm) negatively affected the daily survival rate of Swainson’s thrush nests ($b = -1.39$, 95% CI [-2.72, -0.05]) but we did not find an effect of “heavy” rain events ($>7\text{mm}$; $b = 3.51$, 95% CI [-144.70, 151.73]) (Table 2). We further investigated our rain metrics by quantifying rain intensity as millimeters per hour and found a strong negative relationship on daily survival rate ($b = -0.09$, 95% CI [-0.18, -0.01]; Figure 3). We did not find an effect of cumulative daily precipitation on daily nest survival probability ($b = 0.01$, 95% CI [-0.09, 0.11]). We did not find any support for an interaction effect between rain intensity and cumulative daily precipitation ($b = 0.004$, 95% CI [-0.02, 0.03]), rain intensity and nest age ($b = 0.003$, 95% CI [-0.007, 0.015]), and elevation and rain intensity ($b = -0.00005$, 95% CI [-0.0007, 0.0006]).

In the final stage of our analysis for nests from 2019 and 2021, we compared models of interest using AIC. This revealed two competing models against DSR, the most parsimonious model to be the interaction between elevation and minimum daily temperature against daily survival rate (Table 3). We found some support for the second most competitive model, suggesting that as rain intensity increases, the daily survival rate of Swainson’s thrush decreases ($\Delta \text{AICc} < 4$; Table 3), though it should be noted that this model was within $2\Delta \text{AICc}$ values of the null model.

Discussion

Our results demonstrate that within these northeastern forests, nest survival of passerine birds is negatively influenced by abiotic factors (i.e., intense rain bouts and minimum and average daily temperature) and nests have a lower probability of surviving later in the breeding season. These findings suggest important implications for montane breeding birds as warmer temperatures and more frequent precipitation events are likely to occur due to climate change (Murray et al., 2021; Westra et al., 2014), both factors that have been documented to effect species’ populations in this region (Duclos et al. 2019).

Montane birds face several tradeoffs when breeding along an elevation gradient. For example, DeLuca (2013) documented that blackpoll warblers are more likely to have a successful nest and overall higher annual fecundity at high elevation breeding sites. However, high-elevation breeding pairs of dark-eyed juncos (*Junco hyemalis*) had overall lower nest success, yet their offspring were in better condition than their low elevation population (Bears et al. 2009), potentially because of higher parental investment in these conditions (Badyaev & Ghalambor, 2001; Bears et al., 2009). We predicted that Swainson’s thrush nest survival would have a higher probability of success at high elevations due to the lower predator effects at high elevations (Boyle, 2008; Camfield et al., 2010), and higher success from evidence DeLuca (2013) found in blackpoll warblers, however, our model did not support this prediction. Another purpose for examining this effect was because nest depredation within the White Mountains has historically been affected by red squirrel (*Tamiasciurus hudsonicus*) densities on biennial cone cycles (Townsend et al., 2015), creating challenges for nesting bird species when these fir trees produce mass crops. Specifically, red squirrel densities negatively affected nest survival of American redstarts at a site approximately 64 kilometers west of our study site (Hubbard Brook Experimental Forest, Sherry et al., 2015), raising the possibility that high nest predation is possible during these fluctuating seed-bearing trees (Bergeron et al., 2011; Holmes, 2011). Furthermore, predation from birds may be more active in warmer temperatures (Cox et al., 2013), potentially resulting in unusually higher predation events in warmer, mass crop years. If montane species’ ranges continue to shift upslope (DeLuca & King, 2017; Van Tatenhove et al., 2019), likely in response to climatic influences, they may avoid the increased predation effects at lower elevations but consequently, will be at risk of high elevation abiotic influences. Though we didn’t monitor predator density due to equipment and time constraints, further investigation of predator abundances and mass crops of fir trees along the elevation gradient would help inform how influential predation could be on nest survival of passerine species.

Extreme precipitation events have been shown to negatively influence nest survival of several passerine

species, including in great tits (*Parus major*; Bordjan & Tome, 2014; Schöll & Hille, 2020), northern wheatears (*Oenanthe oenanthe*; Öberg et al. 2015), and in mountain plovers (*Charadrius montanus*; Dinsmore et al., 2002; Dreitz et al., 2012). Additionally, due to the orographic effect (i.e., colder high elevation air forcing clouds to release water), higher montane elevations are likely to receive more rain, prompting us to investigate the relationship between precipitation and nest survival. We found a negative effect of light rain days (0.1-6.9mm daily cumulative, Table 2) and rain intensity on DSR (Table 2, Figure 3) supporting previously documented research and suggesting that rain bouts have negative consequences on DSR of Swainson's thrush. Also, we documented large accumulations of precipitation between 30 June-4 July 2021 (Figure 2b) and had several nest failures throughout the elevation gradient (4 depredated, 4 abandoned) during this time. We examined an interaction effect between seasonal time and daily cumulative precipitation to evaluate if there were more nest failures after this rain event as well as an interaction between nest age and rain intensity to determine if the nest stage was affected by the amount of daily rain, but we did not find support for these relationships. Nests that failed between 30 June-4 July 2021 had nestlings ~5+ days old, and perhaps parents were unable to maintain their own energetic demands in addition to caring for their nestlings (Martin, 1987; Martin, 1995) and chose to renest after the inclement weather passed, though this is risky in that fledglings born later in the season are less likely to survive (Shutler et al., 2006). As the climate continues to warm, more intense precipitation events will become more common (Trenberth, 2011; Westra et al., 2014), putting these montane breeding birds at risk of these effects.

Colder temperatures have been shown to negatively influence nest survival of high elevation breeding bird species (Pierce et al. 2019) and can delay spring insect emergence (Bears et al., 2009; Forrest & Thomson, 2011), especially at higher elevation sites where there may be persisting spring snow (Hahn et al., 2004). Additionally, warm temperatures can promote arthropod abundance (Reneerkens et al., 2011; Tulp & Schekerman, 2008) as well as higher hatching success (Martin, 1987) and fledgling success (Reid et al., 2000). Despite our first prediction, these studies raise the possibility that lower elevation breeding populations may have an advantage over the colder, wetter high elevation nesting pairs. We investigated several different temperature metrics after predicting that minimum daily temperature would have a negative effect on DSR and found strong support for this relationship, in addition to a negative effect of average daily temperature on DSR, but only in conjunction with elevation. This supports our prediction that there are negative effects of temperature on DSR, and further suggests a lower probability of Swainson's thrush nest survival with increasing elevation and colder temperatures. However, Dreitz et al. (2012) reported higher nest success in mountain plovers in cooler temperatures, and perhaps is preferable for high elevation ground nesting breeding birds, since some predators may be more active when temperatures are warmer (Cox et al., 2013).

Warming temperatures and inclement weather events are likely a product of the changing climate (Hamburg et al., 2013; IPCC, 2014; Seidel et al., 2009), resulting in negative direct and indirect effects on species that breed in the White Mountains (Duclos et al., 2019) and causing both upslope and downslope shifts in several montane bird species (DeLuca & King 2017; Van Tatenhove et al., 2019). Although previous literature has documented positive relationships with nest survival and warmer temperatures (Hargrove & Rotenberry, 2011; Martin, 1987; Reid et al., 2000), these climatic effects can trigger major phenological changes and mismatches within bird populations (Leech & Crick, 2007). This could be a disadvantage for single brood species, such as the Swainson's thrush (Mack & Yong, 2020) who rely on certain timing of events (i.e., insect emergence, habitat availability, food abundance) during the breeding season. It should be noted that this phenological phenomenon was not documented at a nearby experimental forest within the White Mountains (black-throated blue warblers, *Setophaga caerulescens* in Hubbard Brook Experimental Forest; Lany et al., 2016). However, Swainson's thrush breed at higher elevations and occupy sensitive habitat, perhaps putting them (and other high-elevation breeding birds) at greater risk of climatic and phenological influences as a result of the warming temperatures.

Evidence within the White Mountains overwhelmingly signals that the climate is changing, leading to more frequent precipitation events in the future (IPCC, 2014; Murray et al., 2021; Wason et al., 2017). Duclos et al. (2019) found that Swainson's thrush populations were directly affected by precipitation, and indirectly influenced by changing vegetation composition due to warming temperatures, though they were uncertain

what underlying mechanisms were driving these relationships. Our results provide insight on this matter, indicating that precipitation and minimum daily temperature negatively influenced nest survival of Swainson’s thrush, thus, potentially affecting their populations. Additionally, Swainson’s thrush rely on specific vegetation composition that includes coniferous tree species such as red spruce and balsam fir (Mack & Yong, 2020). Changes in vegetation composition have occurred in this region (Foster & D’Amato, 2015), though red spruce may be recovering, and thus expanding, due to shifts in land use within this region (Battles et al., 2003). These climatic consequences to Swainson’s thrush populations have both indirect and direct effects (Duclos et al., 2019), and our results provide guidance on the potential underlying mechanistic drivers these effects have.

This study provides evidence that Swainson’s thrush daily nest survival is negatively affected by precipitation (light rain events and rain intensity), as well as minimum and average daily temperature along an elevational gradient. Several factors that were not measured in this study could contribute to nest survival, including habitat structure, predator abundance, and food availability. It is worth noting that other studies have assessed the effects of temporal and abiotic variables on nest survival and had considerably larger sample sizes than us (Dinsmore et al., 2002; Dreitz et al., 2012; Johnson et al., 2018; Pierce et al., 2019) and thus, could be one of the limitations this study faces. As the climate continues to warm and cause more frequent rain bouts, as well as shifts in plant and animal communities that may expose species to factors they are not accustomed to, breeding birds will be at risk of these shifts (Dunn & Winkler, 2010; Parmesan, 2007), especially for species that occupy such restricted niches, like montane birds. Specifically, one species of concern in northeastern forests is the Bicknell’s thrush (*Catharus bicknelli*), a rare and vulnerable species that is facing population declines (Hill et al., 2019; Lambert et al., 2008) and has already been negatively impacted due to climatic effects (Lambert et al., 2008; Rodenhouse et al., 2008). (Freeman & Montgomery, 2015) have documented dominant interspecific aggression from Swainson’s towards Bicknell’s thrush, suggesting that Swainson’s thrush may follow the “push” hypothesis and force Bicknell’s thrush out of their climatic niche, a likely occurrence due to species range shifts (DeLuca & King, 2017). Our inspiration for this study was considered due to the vulnerability the Bicknell’s thrush faces, as well as the finding that Duclos et al. (2019) reported. As we continue to better understand the mechanistic drivers that influence these sensitive montane species, this baseline knowledge will help inform land managers about how passerine birds and their population sizes will cope with the effects of climate change.

Data accessibility statement

Raw data, supplementary materials, and R scripts can be found on Dryad (doi to be determined upon acceptance). Data includes nest survival and daily weather data, supplementary figures and tables, and an rMarkdown of script used to analyze daily survival rate.

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Conflicts of interest

None declared.

Author Contributions

Sarah C. Deckel contributed to conceptual design of the study, organizing, and executing the data collection/field season, all analysis (including interpretation), and writing the draft for this manuscript. William V. DeLuca assisted with conceptualization of the study design, developing field methods and field work, and contributed to final review and editing of the manuscript. Alexander R. Gerson contributed expertise to the manuscript draft and analysis interpretation, as well conceptualization of the study design. David I. King contributed to input on data collection methods, funding opportunities, conceptualization of study design, as well as expertise on the manuscript drafts. All authors gave final approval for this version to be published.

Tables and Figures

Table 1. A list of predictor variables included in analyses of Swainson’s thrush nest survival in the White Mountains, NH. Annotations denote the year it was used: ^aall years, ^b2019 and 2021 only. “DSR” is the response variable, daily survival rate.

Sample 5-column table

Model name (DSR[~])

Model notation

Constant DSR Year Linear time trend Quadratic time trend

Intercept only^a Year^a TimeTrend^a TT^a

Nest Age Elevation Initiation date

NestAge^a Elev^a Init^b

Daily average temperature Daily minimum temperature Daily temperature range

MeanTemp^b MinTemp^b TempRange^b

Daily cumulative precipitation

Precip^b

Rain Events Rain Intensity Yes/No Rain (Binary) Linear time trend * Year Linear time trend * Elevation Elevation * Initiation Date Elevation * Rain Intensity Elevation * Daily Minimum Temp Elevation * Daily Average Temp Nest Age * Rain Intensity Nest Age * Elevation Elevation + TimeTrend

RainEvent^b Intensity^b Binary^b TimeTrendYear^b TimeTrendElev^a ElevInit^b ElevInten^b ElevMin^b ElevMeanT^b NestAgeInten^b NestAgeElev^b ElevTime^b

Table 2. Parameter estimates, standard error (SE), and confidence intervals for daily nest survival for Swainson’s thrush in the White Mountains, NH for all years ($n= 58$; 2016, 2018, 2019, 2021) and for just 2019 and 2021 ($n= 44$). Supported models have 95% CI significance and are denoted when the model’s name is in bold, and models that have some support have 90% significance and are denoted in italics.

All years (2016, 2018, 2019, 2021)

Sample 5-column table

Model

Beta (b)

SE

Lower CI

Upper CI

TimeTrend TT Constant DSR (intercept)

-0.027 -0.0003 0.952

0.014 0.0002 0.007

-0.056 -0.0007 0.934

0.0009 0.00004 0.965

Elev NestAge

0.0005 0.003

0.0007 0.017

-0.0008 -0.031

0.001 0.038

2019 and 2021 only

Model

Beta (b)

SE

Lower CI

Upper CI

Intensity ElevMin ElevMeanT *TimeTrend* TT DSR (intercept only) RainEvent **Light** Heavy TempRange Elev MinTemp Init MeanTemp Precip NestAge

-0.099 -0.0007 -0.0006 -0.030 -0.0003 0.952 — -1.390 3.519 0.063 0.0003 -0.023 -0.007 -0.021 0.010 0.003

0.044 0.0002 0.0001 0.016 0.0002 0.008 — 0.679 75.622 0.054 0.0006 0.056 0.020 0.067 0.053 0.020

-0.185 -0.001 -0.001 -0.057 -0.0008 0.931 — -2.722 -144.70 -0.043 -0.0009 -0.133 -0.047 -0.153 -0.094 -0.036

-0.013 -0.0002 -0.000009 -0.002 0.00008 0.967 — -0.058 151.73 0.169 0.001 0.086 0.032 0.111 0.115 0.043

Table 3. A summary of nest survival model selection results using AIC (Akaike’s Information Criterion) model comparison for Swainson’s thrush in the White Mountains, NH separated between all years ($n = 58$) and just 2019 and 2021 ($n = 44$). 95% CI significance is denoted when the model’s name is in bold, 90% denoted in italics.

All years (2016, 2018, 2019, 2021)

Sample 5-column table

Model (DSR ~)

Model (DSR ~)

Model (DSR ~)

Parameters

AICc

ΔAIC

wi

Deviance

TimeTrend TT **DSR (intercept only)** Year

TimeTrend TT **DSR (intercept only)** Year

TimeTrend TT **DSR (intercept only)** Year

2 2 1 2

189.34 190.10 190.81 191.48

0.00 0.76 1.46 2.41

0.34 0.23 0.16 0.11

185.32 186.08 188.80 187.46

Elev NestAge

Elev NestAge

Elev NestAge

2 2

192.18 192.77

2.84 3.43

0.08 0.06

188.16 188.76

2019 and 2021 only

Model (DSR ~)

Model (DSR ~)

Model (DSR ~)

Parameters

AICc

$\Delta AICc$

w_i

Deviance

ElevMin Intensity DSR (intercept only) **RainEvent** TempRange ElevMeanT Elev MinTemp MeanTemp
Precip

ElevMin Intensity DSR (intercept only) **RainEvent** TempRange ElevMeanT Elev MinTemp MeanTemp
Precip

ElevMin Intensity DSR (intercept only) **RainEvent** TempRange ElevMeanT Elev MinTemp MeanTemp
Precip

4 2 1 3 2 4 2 2 2 2

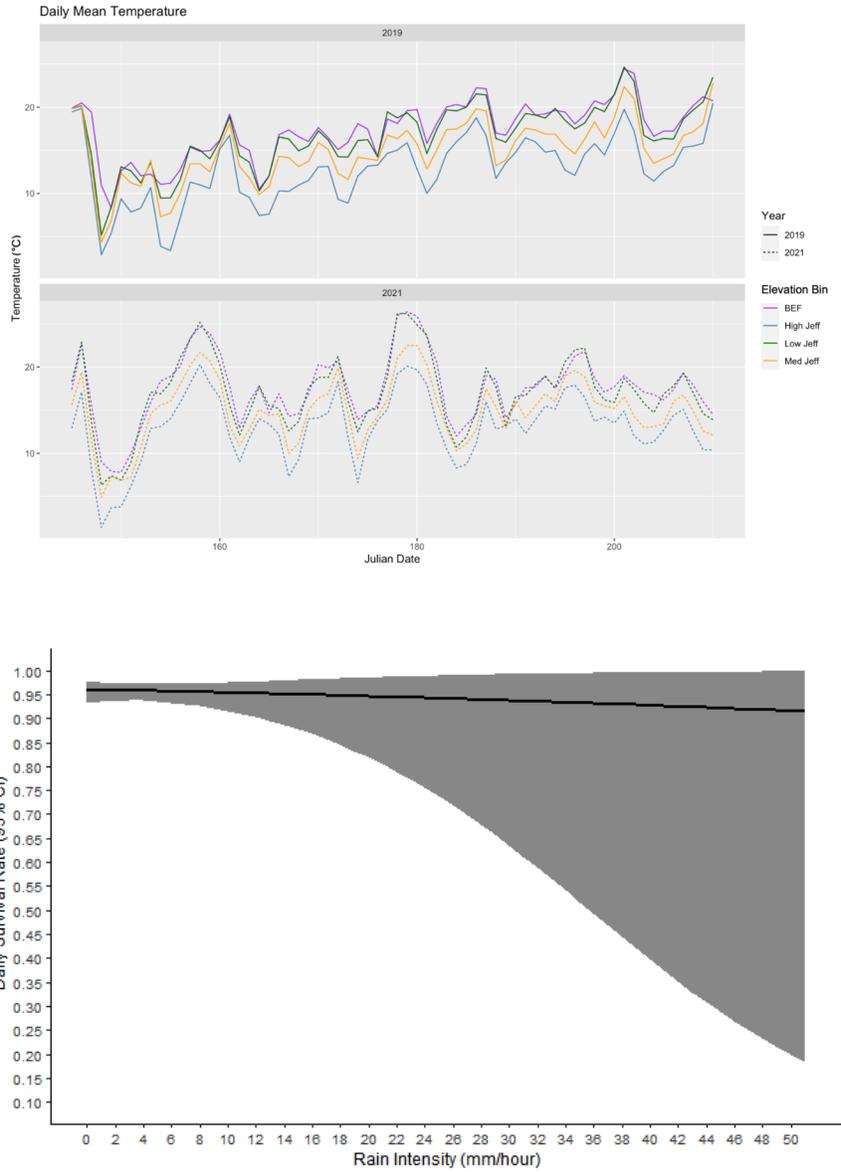
151.49 154.98 155.44 155.71 155.93 156.96 157.18 157.29 157.36 157.41

0.00 3.48 3.94 4.22 4.43 5.46 5.69 5.79 5.86 5.92

0.54 0.09 0.07 0.06 0.05 0.03 0.03 0.03 0.02 0.02

143.42 150.96 153.43 149.67 151.91 148.89 153.16 153.27 153.34 153.39





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