Snowmelt and the nesting phenology of four passerine species in montane wet meadows

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Abstract

Early snowmelt driven by climate change has been associated with changes in phenology for many species. However, there is little research on how montane birds are changing their nesting habits in response to early snowmelt. I looked at the relationship of the date of bare ground and nest onset for Yellow Warbler (*Setophaga aestiva*), Wilson's Warbler (*Cardellina pusilla*), Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*), and Lincoln's Sparrow (*Melospiza lincolnii*) at several sites at varying elevation around Gothic. Using a generalized linear mixed model, I analyzed the relationship between nest onset and the date of bare ground for 2026 and predicted nest onset given the historical mean date of bare ground. Nest onset was found to be significantly influenced by the date of bare ground (95% CI [0.89, 7.69]), as the date of bare ground advanced earlier in the season, nest onset also advanced earlier. Additionally, nest onset advanced 8 days earlier compared to the predicted historical onsets. These results indicate that the breeding timing for these four species is altered by earlier snowmelt, raising concerns for a phenological mismatch between nesting birds and their invertebrate prey.

Introduction

Bird populations have experienced massive declines over the past 50 years. An estimated 3 billion birds have been lost since 1970, with sparrows and wood warblers undergoing the greatest declines (Rosenberg et al., 2019). Reproductive success is an essential requirement for populations to be stable in birds, this happens through successful nesting during breeding seasons (Clark & Martin, 2007). Therefore, understanding how a species changes its nesting habits in response to changes in its environment is crucial to conversation and management initiatives. Climate change is resulting in warmer temperatures and changes in precipitation. In the American Rockies, the mean and maximum temperatures have increased across all elevations (McGuire et al. 2012). Additionally, the number of days favorable for snowfall is predicted to decrease by 30% (Klos et al., 2014). Low snowpack results in changes in phenology; for example, early snowmelt advances the flowering date for many plants (Inouye & Wielgolaski, 2003). A major early constraint for nesting birds is snowmelt date as snow limits available nest sites and invertebrate prey that nesting birds require (Both, 2010). Many species delay nesting onset if snow cover denies access to suitable nest sites (Martin & Wiebe, 2004). In addition, snowmelt date determines the emergence date of the invertebrate prey breeding birds rely on (Finn & Poff, 2008). Consequently, bird species in montane ecosystems have a limited window for reproduction and as a result have shorter and later breeding seasons (Boyle et al., 2016). However, earlier snowmelt dates and thus earlier availability of nest sites and emergence of insects allow birds to access the resources they need much sooner. For example, in the Midwest, the mean nesting start date for Yellow Warbler has advanced by 23 days over the past 140 years (Bates et al., 2023). Earlier nesting has implications for the fitness and survival of young birds as the timing of nesting could be mismatched with peak insect abundance (Bates et al., 2023). It is essential that nesting phenology is documented as earlier snowmelt dates driven by climate change is known to affect the fitness of bird species (Saalfeld et al., 2019; Lameris et al., 2018).

In the Colorado Rockies, Yellow Warbler (*Setophaga aestiva*), Wilson's Warbler (*Cardellina pusilla*), Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*), and Lincoln's Sparrow (*Melospiza lincolnii*) nest in montane wet meadows, primarily composed of willows.

These species are primarily insectivorous and rely on consistent insect populations to successfully rear young (Raley & Anderson, 1990). Phenology within a species can vary based on local temperature and photoperiod (Gienapp et al., 2010), and phenology in montane populations can differ from populations at lower altitudes (Bründl et al., 2020). Additionally, other montane bird species are known to initiate nesting earlier in response to early snowmelt (Hendricks, 2003) However, there is little documentation on the nesting phenology of our four study species in the Colorado Rockies.

Given that snow acts as major constraint for nest onset, I hypothesize that snowmelt date influences the nest onset date of our four study species by restricting the access to nesting and food resources. I predicted that in 2026, a year with low snowmelt, nest onset date would be earlier compared to predicted historical onsets. Furthermore, I predicted that nest initiation dates at higher elevations would be later in the season, as populations at higher elevations generally have later breeding seasons (Boyle et al., 2016).

Methods

Four study sites of varying elevation were used for this study. Each study site is a wet meadow mixed with willow thicket. The area south of Gothic, "South Gothic" was the lowest elevation site (2800m). The second site up valley from Gothic, "East River Valley," was one of the low elevation sites (2900m). The high elevation sites were "Schofield Pass" (3150m) and "North Pole Basin" (3350m) which are approximately 11 km northwest of gothic.

Nests were located using a combination of behavioral observations and rope dragging. For each nest search the observer effort was recorded, including the number of participants and time spent searching. Behavioral observations included carrying nesting material, carrying food, repeated visits to an area, and vocalizations. For example, we observed a Wilson's Warbler carrying food to the base of a willow and consequently found a nest. Rope dragging, a technique in which a rope is dragged through low vegetation to temporarily flush a bird off the nest, allows nests to be found more quickly. Both methods result in a key area to search for a nest. When a nest was located, we recorded its GPS coordinates and whether the nest was active, failed, or succeeded. An active nest still had eggs or nestlings; a failed nest was empty and had evidence of depredation (indicated by damage to the nest); and a succeeded nest had evidence of a fledging, indicated by no damage the nest and often nearby fledglings and defensive parent behavior. Nests were checked every three days after the initial finding. Eggs were carefully removed from the nest and candled, meaning holding an egg up to the sun against a Styrofoam tube, and estimated how much light passed through. The amount of light that passed through the egg was used to determine the stage of development, the less light that passed through, the more developed the egg was. Egg development was recorded in three categories: low, medium and high. If a nest contained live young, the age was estimated by feather development. When a nest was found empty during a check and there was no camera we inferred if the nest was predated or the birds fledged, based on the age of the nestlings and the condition of the nest. Nest initiation date was estimated by using the age of the nestlings and adding the average incubation period for each species. The incubation and nestling period used was 12 days and 9-12 respectively for Lincoln's Sparrow, White-crowned Sparrow, Yellow Warbler, and Wilson's Warbler (Ammon & Gilbert, 2020; Chilton et al., 2020; Pandolfino et al., 2023; Valdez-Juárez et al., 2025). If a nest failed before making it to the nestling stage, the initiation date was estimated from the development of the eggs, by splitting the development into thirds. For example, if the egg development was medium, the estimated age is 8 days.

The date of first bare ground was used as the indicator for snowmelt. The historical mean date of bare ground from 1993 – 2022 was sourced from the RMBL Spatial Data Platform (Breckheimer 2022), while the forecasted date of bare ground for 2026 was provided by Ian Breckheimer (personal communication, 2026). The date of bare ground was extracted for each nest GPS point using the terra package in RStudio (Hijmans et al. 2026; Posit team 2025). The R packages sf (Pebesma & Bivand, 2023), tidyverse (Wickham et al., 2019), and dplyr (Wickham et al., 2023) were used to create a usable data frame suitable for modeling.

We created a generalized linear mixed model using the R package glmmTMB (Brooks et al., 2017; McGillycudd et al., 2025) where date of nest onset was the response variable, and predictors included random effects of species (t) and site (p) and a fixed quadratic effect of date of bare ground. Our model formula was: $onset = \alpha + \beta_1 snowmelt + \beta_2 snowmelt^2 + t + p$. Statistical significance was assessed based on coefficient estimates having p-values < 0. 05. Then, we fitted the model onto the historical date of bare ground data for the same species and sites to see whether nest initiation date changed.

Results

A total of 43 nests were included in this study (Table 1). Mountain White-crowned Sparrow was the most abundant with 14 nests, followed by Wilson's Warbler with 13 nests, Yellow Warbler with 10 nests, and Lincoln's Sparrow with 6 nests. The proportion of total nests fledged was 0.6. The proportion of nests fledged for Lincoln's and Mountain White-crowned Sparrow was 0.5, while the proportion of nests fledged for Wilson's and Yellow Warbler was 0.7 for both. The average nest onset date across all species was June 13th. The average nest onset dates for Lincoln's and Mountain White-crowned Sparrow were June 18th and June 15th respectively. The average nest onset dates for Wilson's and Yellow Warbler were June 11th.

South Gothic was our lowest elevation site at 2800m (Table 2). South Gothic had a total of 12 nests, 0.5 of which fledged, and an average nest onset date of June 9th. East River Valley had an elevation of 2900m, a total of 17 nests, 0.8 was the proportion of nests fledged, and an average nest onset date of June 12th. Schofield Park had an elevation of 3150m, a total of 9 nests, 0.3 of those nests fledged, and an average nest onset date of June 18th. North Pole Basin was our highest elevation site at 3350m. North Pole Basin had a total of 5 nests, the proportion of fledged nests was 0.4, and the average nest onset date was June 20th. The 2026 and historical date of bare ground for South Gothic was April 29th and May 16th respectively. For East River Valley it was May 6th and May 24th. The Schofield Park averages were May 24th and June 12th. Finally, the North Pole Basin averages were May 28th and June 18th.

There is a statistically significant relationship between snow melt date and nest onset date: as snow melt date gets later in the season, nest onset also becomes later (95% CI [0.89, 7.69]. Little variance was explained by species (9.3) and even less variance was explained by site (6.7×10^{-8}) The predicted nest onset date for all four species given 2026's forecasted date of bare ground (Figure 1) was approximately 8 days earlier compared to the historical mean date of bare ground from 1993 – 2022 (Figure 2-3).

Discussion

For 2026, the date of bare ground was found to influence the nest onset date for our four study species; as the date of bare ground became earlier in the season, the nest onset date also became earlier. When we used the model to predict nest onset date based on the date of bare ground averaged across 1993-2022, we found that the nest onset date was 8 days later compared to predicted 2026 nest onset dates. This is consistent with our predictions and previous findings (Hendricks, 2003), that nest onset date would advance earlier into the season with earlier snowmelt. Snowpack acts as a constraint to nesting as it limits nesting sites and the availability of food (Both, 2010). An earlier shift in nest onset suggests that our study species can respond to changes in climate conditions.

Site location and species had little influence on the nest onset date, contrary to my predictions. Given our general observations (snow present at North Pole Basin in June) and previous research which suggests that bird populations at higher altitudes have shorter and later breeding seasons (Boyle et al., 2015), I predicted the higher elevation sites to have a later nesting onset. However, the absence of this signal may be due to the extremely early snowmelt at the high elevation sites allowing for earlier nesting and thus a more uniform breeding season across all elevations

There is a concern that an earlier breeding season may cause a phenological mismatch for our study species and peak insect abundance. One study found that species that advanced nesting onsets earlier in the season were experiencing the greatest declines and that nesting was less aligned with insect abundance (Phillimore et al., 2016). Another study found that species that are increasing the duration of their breeding season are nesting before peak insect abundance (Møller et al., 2010). Interestingly, earlier breeding seasons at higher elevations increase reproductive success in Mountain Chickadees (*Poecile gambeli*) (Whitenack et al., 2024). Further research is needed to determine that our study species are nesting before peak insect abundance.

A factor that could also be influencing nest onset date is the timing of green-up or the blooming of plants. Several on Eurasian Blue Tits (*Cyanistes caeruleus*) found that birch budburst and oak green-up were significant predictors of nest initiation (Shutt et al., 2019; Cole et al. 2015). Future research into the relation between green-up and nesting onset for our study species would clarify whether green-up or snowmelt date is a better predictor of nesting phenology. Another topic of future research is the influence of climate change on predation rates. Nest success rates were low, with the sparrow species having a success rate of 50%, suggesting heavy predation. Ibáñez-Álamo et al. (2015) suggests that climate changed induced warming temperatures could increase predation events from ectothermic predators such as snakes. However, early green-up times resulting from climate change increase concealment for nesting birds and may decrease predation rates (Halupka et al., 2023). The relationship between predation rates and climate change is worth exploring as it may have negative consequences for reproductive success.

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Tables

Table 1: The number of nests, proportion of nests fledged, and the average nest onset date for our four study species.

Species	Number of nests	Proportion of nests fledged	Average date of nest onset
Lincoln's Sparrow (*M. lincolnii*)	6	0.5	6/18/26
Mountain White-crowned Sparrow (*Z. l. oriantha*)	14	0.5	6/15/26
Wilson's Warbler (*C. pusilla*)	13	0.7	6/11/26
Yellow Warbler (*S. aestiva*)	10	0.7	6/11/26
Total	43	0.6	6/13/26

Table 2: The elevation, number of nests, proportion of nests fledged, average nest onset date, and the 2026 and historical average date of bare ground categorized by site.

Site	Elevation (m)	Number of nests	Proportion of nests fledged	Average date of nest onset	Average date of bare ground (2026)	Average date of bare ground (historical)
South Gothic	2800	12	0.5	6/9/26	4/29/26	5/16
East River Valley	2900	17	0.8	6/12/26	5/6/26	5/24
Schofield Park	3150	9	0.3	6/18/26	5/24/26	6/12
North Pole Basin	3350	5	0.4	6/20/26	5/28/26	6/18

Figures

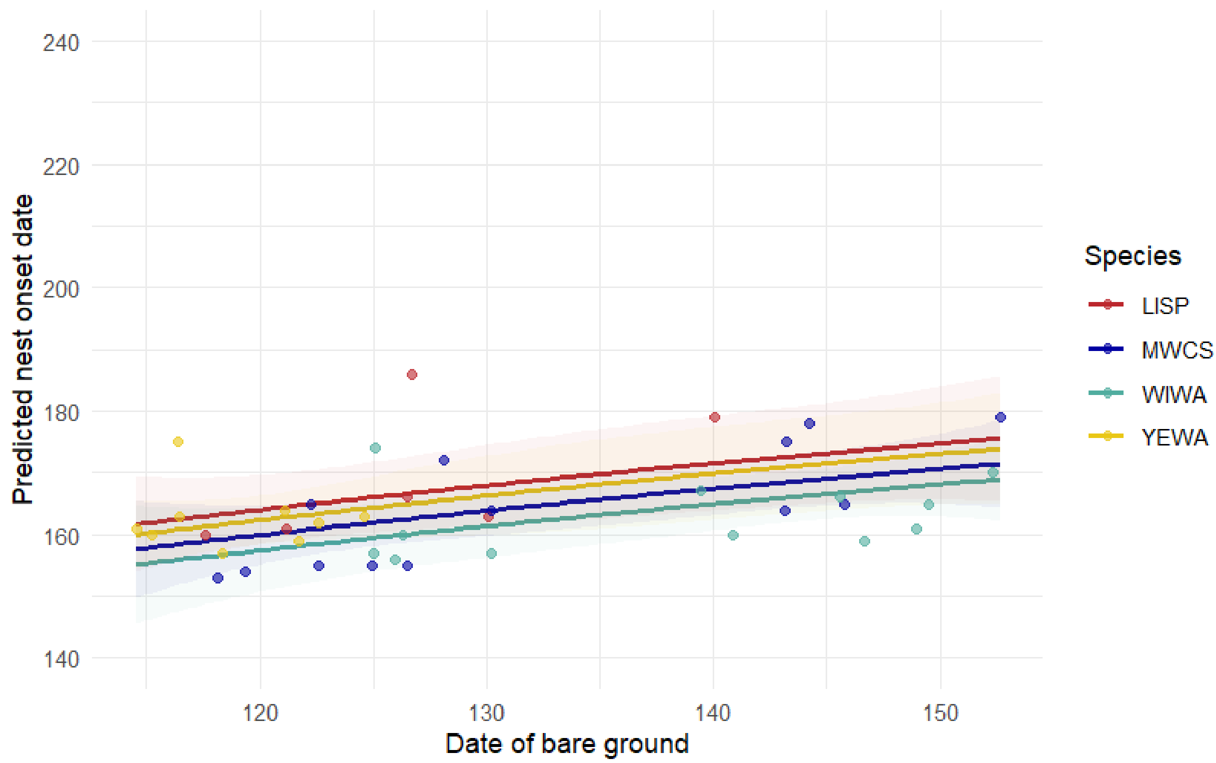

Fig. 1. Marginal effect of snowmelt date as a predictor of nest onset date in generalized linear mixed effects model showing predicated nest onset date in Julian days given the forecasted date of bare ground in Julian days for 2026. The random effects are species and site, and the fixed effect is date of bare ground. Error ribbons represent a 95% CI.

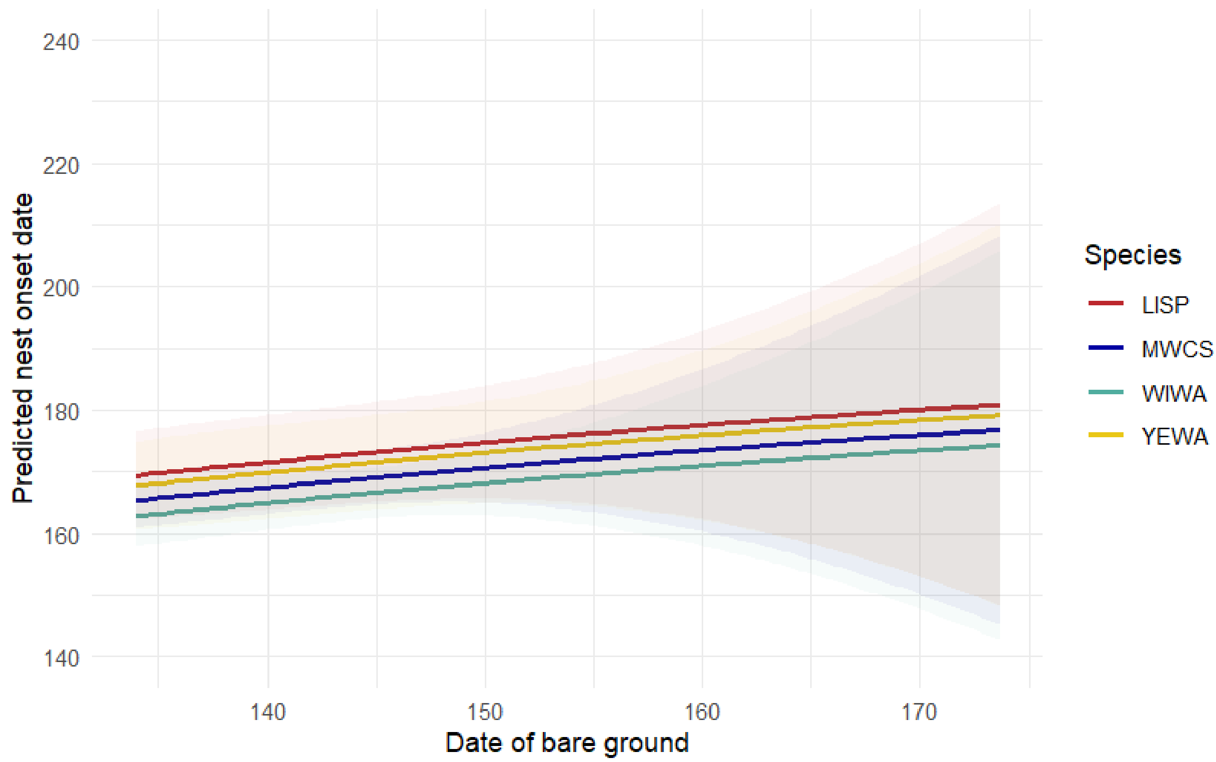

Fig. 2. Marginal effect of snowmelt date as a predictor of nest onset date in generalized linear mixed effects model showing predicated nest onset date in Julian days given the historical mean of bare ground in Julian days for 1993-2022. The random effects are species and site, and the fixed effect is date of bare ground. Error ribbons represent a 95% CI.

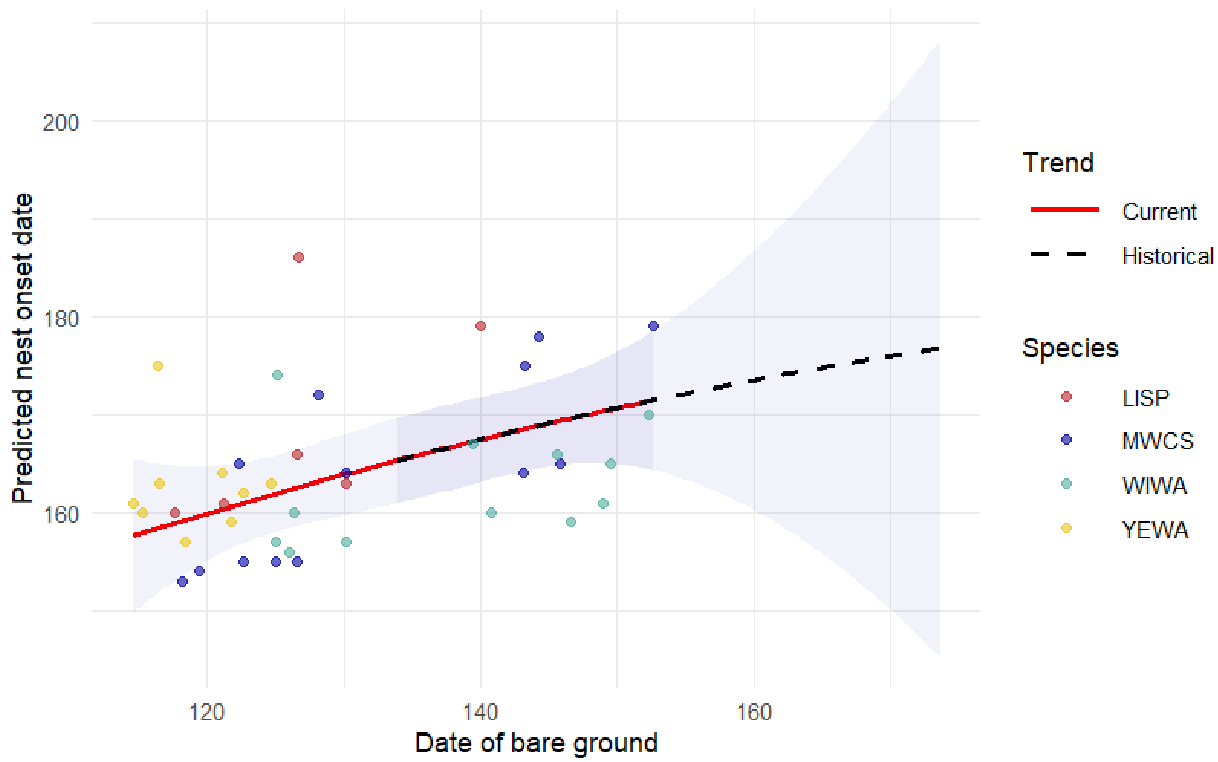

Fig. 3. Marginal effect of snowmelt date as a predictor of nest onset date in generalized linear mixed effects model showing predicated nest onset date for Mountain White-crowned Sparrow in Julian days given the forecasted date of bare ground in Julian days for 2026 (red) and the historic mean date of bare ground for 1993-2022 (black, dashed). The random effects are species and site, and the fixed effect is date of bare ground. Error ribbons represent a 95% CI.