Taming the temperature: Sagebrush songbirds modulate microclimate via nest-site selection

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ABSTRACT
Understanding species’ responses to temperature via behavior, and the factors affecting the extent of behavioral responses, is a critical and timely endeavor given the rapid pace at which the climate is changing. The young of altricial songbirds are particularly sensitive to temperature, and parents may modulate temperatures at nests via selection of nest sites, albeit to a largely unknown extent. We examined whether sagebrush-obligate songbirds, that reproduce within an open ecosystem with wide temperature fluctuations and span a range of body sizes, selected their nest sites on the basis of temperature. We further investigated whether nest predation risk and ambient conditions modulated temperature-based choices. We placed temperature loggers at nest sites and in unused but available nest niches and nest shrubs along a known predation-risk gradient and used nearby weather stations to determine ambient temperatures. The two smaller-bodied birds, Brewer’s Sparrow (Spizella breweri) and Sagebrush Sparrow (Artemisiospiza nevadensis), selected nest shrubs and niches that were warmer and less variable relative to unused sites whereas the larger bodied species, Sage Thrashers (Oreoscoptes montanus), did not. Brewer’s Sparrows and Sage Thrashers dampened selection for warmer nest sites when temperatures experienced during the nest-site prospecting period were warmer. None of the three species altered nest-site selection with respect to temperature in response to ambient temperature variability or our index of nest predation risk. The microhabitat characteristics that most influenced temperatures at nests varied across species. Our results suggest that songbirds can modulate temperatures at nests to some extent, and such responses can vary depending on the conditions experienced prior to nest initiation. Responses also varied across species, likely reflecting different physiological tolerances. The extent to which breeding birds will be able to continue to proximately influence temperature via nest-site choices likely will depend on the extent and rate of future climatic shifts.

Keywords: Brewer’s Sparrow, microclimate, nest predation, nest-site selection, Sagebrush Sparrow, Sage Thrasher, temperature

LAY SUMMARY

• Due to rapid changes associated with climate change, a better understanding of how behavior may help wildlife adapt will be critical.
• Songbirds are sensitive to temperature during the breeding season, as there is a tight range of temperatures under which optimal development of young occurs.
• Using songbirds in the sagebrush steppe, we examined how birds may be able to use nest-site selection to help mitigate within-season variation and nesting temperatures.
• Sagebrush songbirds selected nest sites based on temperature, but the extent varied with body size, spatial scale, and temperatures experienced.
• Nest site selection may help buffer some negative effects of a changing climate, provided that the rate and extent of temperature change does not outpace the capacity of birds to respond.

Moderar la temperatura: las aves canoras vinculadas a la vegetación de Artemisa modulan el microclima a través de la selección del sitio de nidificación

RESUMEN
Comprender las respuestas de las especies a la temperatura a través del comportamiento y los factores que afectan el alcance de las respuestas del comportamiento es un esfuerzo crítico y oportuno dado el rápido ritmo al que está
INTRODUCTION

Wildlife species employ a variety of mechanisms to cope with extreme weather conditions (Grant et al. 2017). Simultaneously, climate is changing at an unprecedented pace, with diverse consequences for wildlife and their habitats (Moritz and Agudo 2003, Parmesan 2006, Stocker et al. 2013). Given the rapid nature of shifting climatic regimes, most species will not be able to adapt via the evolution of new traits (Sih et al. 2011). Understanding of other potential means by which organisms proximately buffer weather conditions is therefore increasingly important. Species may respond via shifts in range, though range shifts are less plausible for some taxa, including habitat specialists (Chen et al. 2011). Alternatively, individuals may behaviorally modulate the effects of extreme weather conditions, for example via behavioral plasticity in habitat choices (e.g., Hall et al. 2016), albeit to an unknown extent for most taxa. Understanding how individuals within populations of concern may employ behavioral tactics to limit exposure to adverse weather conditions will be critical for conservation assessments and evaluations of the potential ramifications of a changing climate for wildlife. Individuals and populations that are able to respond to local weather may be better suited to respond to the extreme temperature changes and variability associated with climate change.

Physiological constraints associated with body size can influence the degree to which species are affected by weather conditions (Riesenfeld 1981). Relationships between temperature and body size have been studied extensively, as body size affects surface-to-volume ratios and other traits that can influence an organism’s capacity to shed and retain heat. Indeed, declining body size may increase resilience to climate change because of its effect on thermoregulation and energetics (Gardner et al. 2011). How body size may affect proximate habitat choices in relation to temperature within latitudes will inform predictions of how responses to temperature shifts may manifest across populations and species.

Selection of a reproductive site, in particular, is a critical habitat decision in terms of survival prospects for altricial offspring (Li and Martin 1991, Martin 1998, Mueller et al. 2019). Reproductive site selection, for example, affects the microclimatic environment to which parents and young are exposed, and can be a plastic behavior (e.g., Chalfoun and Martin 2010a). Embryonic development occurs within a tight range of temperatures (36–40°C), and prolonged exposure outside of the optimal range can result in deformities, delayed hatching, or mortality (White and Kinney 1974, Webb 1987). No such range has been established for altricial nestlings, though they too have a limited ability to thermoregulate during the early nestling period, and rely on parental care to maintain tolerable body temperatures (Baldwin and Kendeigh 1932, O’Connor 1975). As nestlings develop their ability to thermoregulate, moreover, exposure to extreme temperatures causes stress and increased energy expenditure to maintain body temperature, which could otherwise be used for growth (Visser 1998, Dawson et al. 2005, Fairhurst et al. 2012).

The extent to which songbirds select nest sites that modulate temperature under different contexts, and at which spatial scales remains unclear (Rauter et al. 2002, Robertson 2009, Germain et al. 2015, Høyvik Hilde et al. 2016). Birds
must balance multiple potential selective pressures when choosing nest sites (Chalfoun and Schmidt 2012), and those selective pressures can vary across spatiotemporal scales (Chalfoun and Martin 2007, Streby et al. 2014).

Predation is the primary cause of complete nest mortality for songbirds (Ricklefs 1969, Martin 1995), and nest-site selection in relation to predation risk has been studied extensively (Martin and Roper 1988, Martin 1993, Forstmeier and Weiss 2004, Chalfoun and Schmidt 2012, Ibáñez-Alamo et al. 2015). Predation risk may be difficult for adults arriving at breeding grounds to assess during a given year, however, because of spatiotemporal variation in predation risk and the diverse predator assemblages to which nesting songbirds are often exposed (Chalfoun and Martin 2010b). By contrast, temperature may be more assessable based on ambient conditions experienced. If weather conditions during prospecting for a nest site and the ensuing weeks are reasonably correlated (or were historically), ambient weather could be a reliable cue for behavioral choices. Findings regarding how nest predation risk may affect selection for microclimate, moreover, have been mixed. Although predation risk may be difficult to assess in the early season, adults may alter decisions as they gather more information on predation risk, foregoing selection driven by other stressors such as microclimate (Forstmeier and Weiss 2004, Fontaine and Martin 2006). Conversely, other species demonstrated no alteration of selection for microclimate given predation risk (Robertson 2009), or seemed to favor selection for microclimate over predation risk as the season progressed (Tieleman et al. 2008). Simultaneous examinations of how nest predation risk and microclimate influence nest-site selection throughout the nesting season will help tease apart the influence of multiple selective pressures on nest-site selection.

Species that inhabit open, arid systems with extreme weather variability—such as the sagebrush steppe of North America—may be particularly vulnerable to climatic factors at nest sites. Climatic predictions for the sagebrush steppe, moreover, include increased average temperatures, decreased precipitation, and increased frequency of extreme weather events and variability (Stocker et al. 2013) which can cause offspring mortality (Hightower et al. 2018). Simultaneously, sagebrush habitats also have been highly converted and altered by many human activities (Knick et al. 2003), which has been associated with declines in sagebrush-obligate songbirds: Brewer’s Sparrow (Spizella breweri), Sagebrush Sparrow (Artemisiospiza nevadensis), and Sage Thrasher (Oreoscoptes montanus) (Sauer et al. 2017). Mechanistic investigations of the effects of habitat change on sagebrush songbirds have revealed linkages between rates of nest predation and surface disturbance associated with energy development (Hethcoat and Chalfoun 2015a, b; Sanders and Chalfoun 2018). Sagebrush songbirds, therefore, provided an ideal system with which to simultaneously assess nest-site selection in relation to temperature variability and the risk of nest predation in situ, via the use of surface disturbance as a proxy for predation risk. Sagebrush songbirds also span a range of body sizes—Brewer’s Sparrows, 10–13 g (A. D. Chalfoun, personal observation), Sagebrush Sparrows, ~19 g (Martin and Carlson 2020), and Sage Thrashers, ~45 g (Reynolds et al. 2020)—which enabled the examination of nest-site selection in relation to body size.

We tested the hypothesis that songbirds such as sagebrush-obligates, that inhabit open, exposed environments select nest sites that dampen temperature variation and exposure to extreme temperatures at multiple spatial scales, to varying extents across species that vary in body size. Our specific objectives, followed by their respective predictions, were to examine:

1) The habitat characteristics that most affected temperature at nests. Here, we predicted habitat attributes that provide concealment from solar insolation and convection would dampen nest site temperatures and temperature variability (Table 1).

2) The extent to which songbirds spanning a gradient of body size modulate temperatures at the nest via nest-site selection at multiple spatial scales including the nest shrub and nest niche (specific space within the shrub where the nest is placed). We predicted that the larger-bodied species (Sage Thrasher) would select cooler nest sites relative to unused sites, whereas the smaller species (Brewer’s Sparrow and Sagebrush Sparrow) would demonstrate selection for nests sites with less variable temperatures.

3) What other factors (nest predation risk and temperature conditions during prospecting) may alter selection of nest sites on the basis of temperature. First, we predicted that all three species would be more likely to

### TABLE 1. A priori hypotheses for which microhabitat characteristics most affect microclimate at the nest sites of Brewer’s Sparrows, Sagebrush Sparrows, and Sage Thrashers, and why. The second column includes the physical attributes anticipated to be influenced by habitat metrics

| Metric                          | Hypothesis                                               |
|---------------------------------|----------------------------------------------------------|
| Nest height                     | Amount of convection around the nest                     |
| Nest orientation                | Time of day the nest receives the most solar insolation   |
| Distance to shrub edge          | Amount of convection around the nest                     |
| Shrub vigor                     | Amount of solar insolation the nest receives             |
| Overhead cover                  | Amount of solar insolation the nest receives             |
| Average side cover              | Solar insolation and convection                          |
| Surrounding shrub density       | Convection around the nest                               |
select nest sites that were cooler in terms of temperature relative to unused sites when they experienced hotter average temperatures during the prospecting period, and less variable in terms of temperature when they experienced high-temperature variability during the prospecting period.

Second, we predicted that if songbirds could simultaneously assess the risk of nest predation, all three species should decrease selection of nest sites for temperature with increased predation risk (herein indexed by established and inverse relationships between surface disturbance associated with natural gas development and nest survival).

METHODS

Study Area
We conducted our study in the Upper Green River basin of Sublette County, Wyoming, USA during May to August, 2017–2018. We collected data within 12 25-ha plots, with 6 plots located on the Pinedale Anticline Project Area (42.776861°N, –109.8832°W; hereafter, PAPA) and 6 plots on the Jonah gas field (42.473027°N, 109.57994°W). Plots within each gas field were separated by ≥2 km (range: 2–6), and spanned a gradient of energy development intensity as indexed by surrounding surface disturbance, ranging from 0 to 38 ha within 1 km² of study plot centers (Hethcoat and Chalfoun 2015b). Plots were dominated by big sagebrush (Artemisia tridentata) with elevation ranging from ~2,180 to 2,250 m. Average temperature from May 1, 2017 to August 1, 2017 was 13.5°C (minimum = −6.56°C, maximum = 30.56°C, variance = 68.9, standard deviation = 6.7°C) for the PAPA and 13.2°C (minimum = −6.68°C, maximum = 30.56°C, variance = 62.2, standard deviation = 6.3°C) for the Jonah. Temperatures during the same time span in 2018 averaged 14.6°C for both gas fields (minimum = −4.94°C for the PAPA and −6.15°C for the Jonah, maximum = 32.73°C for the PAPA and 31.67°C the Jonah, variance = 64.6 for the PAPA and 60.1 for the Jonah, and standard deviation = 6.8°C and 6.6°C, respectively). Temperatures were highly variable from May through June 2017 and 2018, whereas July temperatures were hotter and less variable at both gas fields (Figure 1).

We searched each plot every one to three days for active nests of the three focal species from May 1 through July 31 each year. Nests were located using systematic searches and behavioral observations of adults. We monitored nests every two to three days until success or failure (Martin et al. 1997).

Habitat Characteristics and Nest Microclimate
We placed HOBO U23 Pro v2 External Temperature Data Loggers (Onset Computer Corporation, Bourne, Massachusetts, USA; hereafter, loggers) in the nest wall of a subset of active nests of all three species. Loggers were placed flush with the surface of the nest (Figure 2), with the orientation of the logger aligned with that of the nest to record temperatures that mimicked those experienced by the adults and young in the nest, without being influenced by their body heat. Loggers recorded temperature every 15 min until the nest either fledged or failed. We included only nests that recorded temperatures for at least 9 days for Brewer’s Sparrows, 10 days for Sagebrush Sparrows, and 11 days for Sage Thrashers (approximately half of the total nesting period for each species) to ensure a sufficient representation of the average temperature and temperature variability experienced at the nest.
Nest site selection and microclimate

We assessed habitat metrics at nest sites that we hypothesized could influence the microclimate at nests (Table 1). At all nest locations, we recorded nest height, maximum shrub height (excluding inflorescences), shrub width, shrub length, crown vigor, nest concealment, distance from the main stem to the outer rim of the nest cup, and the cardinal direction of the nest cup from the main stem that was then categorized as NE, EW, SE, SW (Lloyd and Martin 2004). Nest concealment was a visual estimate taken from 1-m directly above the nest cup and from each of the cardinal directions (Martin and Geupel 1993). We used a visual estimate of the percent of the shrub crown that was alive relative to the overall shrub size for crown vigor. For all ocular estimates, we calibrated among crew members at the start of each day to ensure accuracy and consistency among sites. At the patch scale, we quantified the density of all shrubs >20 cm by counting the total number within a 5-m radius around nests.

Nest-Site Selection and Nest Temperature

To assess the extent to which birds selected nest sites on the basis of temperature, we placed Thermochron iButton data loggers (Maxim Integrated Products, Sunnyvale, California, USA; hereafter, iButtons) at a subset of nest sites no more than 3 weeks after success or failure. We removed nest cups at nest sites to control for any thermoregulatory benefits provided by the nest cup. To assess selection based on temperature at the shrub scale, we placed two iButtons in randomly-selected, potential nest shrubs within a 5-m radius of the nest shrub. Randomly selected shrubs in the surrounding area were at least 30% alive and contained ample overhead concealment and a nest niche that would have allowed birds to have nested where we placed the iButton (Chalfoun and Martin 2009, Hethcoat and Chalfoun 2015a). We did not attempt to select random sites based on orientation, shrub height or width, concealment, or other properties of the used shrub given observed variation in nest-site selection (T.M. Scherr, personal observation). To assess nest-site selection within the nest shrub, we placed an iButton in an unused but available nest niche within the same shrub. The iButtons recorded temperature every hour for a 48-hr period. Changes in habitat characteristics during the interim between nest completion and temperature assessments that would have altered the relative temperatures for used and paired unused sites were unlikely given the slow growth of big sagebrush.

Other Factors Associated with Selection for Temperature

We defined the nest-site prospecting period as the several days preceding the commencement of nest building. Most pairs within the study area constructed their nests within 3–4 days. We, therefore, assessed the ambient temperatures and temperature variation experienced during prospecting by summarizing temperature data over the 4-day period beginning 7 days prior to nest initiation (day first egg was laid) for each nest. We used hourly temperature data from the Wyoming Agricultural Climate Network data from the Daniel, Wyoming station (Daniel 8S) for sites located on the PAPA and data from the Boulder, Wyoming station (Boulder 2SE) for sites on the Jonah gas field (Figure 1). The exact data of nest initiation was known in some instances. When the exact date was unknown, we back-calculated using average estimates of incubation length.

We used surface disturbance as a proxy for predation risk (Hethcoat and Chalfoun 2015b, Sanders and Chalfoun 2018). The extent of surface disturbance within 1 km² was calculated for each nest site using National Agricultural Imagery Program files (USDA Geospatial Data Gateway 2015) in ArcGIS 10.0 (ESRI 2011) and included gas field roads, well pads, and reclaimed areas.

Statistical Analyses

All statistical analyses were conducted in Program R 3.4.2 (R Core Team 2017). We assessed which habitat metrics most affected temperatures and temperature variability at nests by creating a suite of generalized linear mixed models (GLMMs) based on a priori hypotheses (Table 1). We included models with and without the date of nest initiation to account for potential differences based on time of season. We then ranked models using Akaike’s Information Criterion adjusted for small sample sizes (AICc) to determine the top-ranking metrics and reported models ≤2 ΔAICc from the top model for each model suite.
To examine relationships between nest-site selection and temperature for each species we used conditional logistic regression, given our paired design of used compared with unused but available nest sites. We used mean temperature and temperature variance as fixed effects and included Nest ID as a stratum and study plot as a random effect. We ranked model performance using Quasi-likelihood Information Criterion (QICc) and report the top-ranking models.

To determine whether other factors influenced nest-site selection on the basis of temperature, we used GLMMs with a gaussian distribution to allow a random intercept of study plot, with the difference in mean temperatures and temperature variance between used and unused nest sites (Temperature\(_{unused} - \text{Temperature}_{used}\)) as the response variables, and surface disturbance (a proxy for nest predation risk) and prospecting temperature and temperature variance as independent variables. We assessed model assumptions including data linearity and independence, and whether residuals were normally distributed, via residual plots, quantile-quantile plots, and autocorrelation correlograms. We then created a suite of models based on our hypotheses, resulting in 5 models for each spatial scale. Models for both mean temperature difference and temperature variance difference included the null model, year, prospecting temperature and year, surface disturbance and year, and a global model. We ranked models using Akaike’s Information Criterion adjusted for small sample sizes (AICc). We report the full AICc model suite (Table 4), and model-averaged models ≤2 ΔAICc from the top model to obtain beta estimates and account for model uncertainty. We report the full average beta coefficients for model-averaged models. Although some concerns exist for model averaging (Cade 2015, Banner and Higgs 2016), we did not have multicollinearity among our variables, and we approached our analyses with explicit, thorough a priori hypotheses to create our candidate models and guide the model selection process. We report the \(R^2\) for the global model.

### RESULTS

We placed data loggers at 87 nests (43 Brewer’s Sparrow, 20 Sagebrush Sparrow, and 24 Sage Thrasher) during the 2017 breeding season, and 59 nests (21 Brewer’s Sparrow, 19 Sagebrush Sparrow, and 19 Sage Thrasher) during 2018. We placed iButtons at 132 nests (57 Brewer’s Sparrow, 37 Sagebrush Sparrow, and 38 Sage Thrasher) during the 2017 breeding season, and 130 nests (48 Brewer’s Sparrow, 43 Sagebrush Sparrow, and 39 Sage Thrasher nests) during 2018. Data from one sage thrasher nest from 2017 were omitted due to iButton malfunction.

### Habitat Characteristics and Nest Microclimate

#### Brewer’s Sparrows

The average nest temperature for Brewer’s Sparrows was 20.3°C (minimum = −7.7°C, maximum = 55.0°C, standard deviation = 9.5°C). Average nest-site temperatures at Brewer’s Sparrow nests decreased with shrub density, especially later in the season (\(\beta = 0.11\); Table 2). Temperature variability increased with shrub vigor, but less so later in the season (\(\beta = −0.04\); Table 2). The intercept model, however, ranked within 2 ΔAICc of the top model (Table 2).

#### Sagebrush Sparrows

The average nest temperature for Sagebrush Sparrows was 19.5°C (minimum = −8.3°C, maximum = 58.3°C, standard deviation = 10.4°C). Average nest-site temperatures at Sagebrush Sparrow nests decreased with shrub density, especially later in the season (\(\beta = 0.08\); Table 2). Temperature variability decreased at nests with more overhead cover (\(\beta = −0.33\)) and higher shrub vigor (\(\beta = −0.45\), within 2 ΔAICc of the top model; Table 2).

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**TABLE 2.** Competing AICc models demonstrating the effects of microhabitat metrics on average temperature and temperature variability recorded at Brewer’s Sparrow, Sagebrush Sparrow, and Sage Thrasher nests, with all models ≤2 ΔAICc from the top model reported. All nests were located in 2017 and 2018 within or adjacent to the Jonah natural gas field and the Pinedale Anticline Project Area, Wyoming, USA. Log(L) are the log-likelihood values, ΔAICc is the difference in Akaike’s information criterion (AICc) values between the top-fitting model and the reported model, and \(w\) is the Akaike weight of each model representing fit.

| Species             | Response variable | Model                              | log(L)  | ΔAICc | \(w\) |
|---------------------|-------------------|------------------------------------|---------|-------|-------|
| Brewer’s Sparrow    | Average temperature | Initiation date * shrub density | −122.51 | 0     | 0.67  |
|                     |                   | Initiation date * shrub vigor     | −299.73 | 0     | 0.34  |
|                     |                   | Intercept                         | −304.13 | 1.78  | 0.14  |
|                    | Variance          | Initiation date * shrub density   | −85.59  | 0     | 0.54  |
|                    |                   | Overhead cover                    | −181.02 | 0     | 0.41  |
| Sagebrush Sparrow   | Average temperature | Initiation date * distance to shrub edge | −78.72 | 0 | 0.41 |
|                    |                   | Average side cover                | −79.26  | 1.09  | 0.24  |
|                    | Variance          | Shrub vigor                       | −181.77 | 1.51  | 0.19  |
|                    |                   | Initiation date * average side cover | −170.44 | 0 | 0.17 |
| Sage Thrasher       | Average temperature | Shrub vigor                       | −167.93 | 0.29  | 0.15  |
|                    |                   | Initiation date * average side cover | −171.87 | 0.42  | 0.14  |
|                    | Variance          | Initiation date * shrub density   | −168.18 | 0.80  | 0.11  |
|                    |                   | Initiation date * shrub vigor     | −168.42 | 1.27  | 0.09  |
The average nest temperature for Sage Thrashers was 17.4°C (minimum = −9.0°C, maximum = 52.2°C, standard deviation = 9.4°C). Average temperatures at thrasher nests decreased with increasing distance of the nest to the edge of the shrub (β = −0.001) and less side cover (β = −0.001), to a lesser extent during the late season (Table 2). Temperature variability at thrasher nests tended to decrease with shrub vigor (β = −0.24) and side cover (more so in the late season; β = 0.01), though three other models fell within 2 ΔAICc of the top model, including the intercept (Table 2).

**Nest-Site Selection and Temperature**

Brewer’s Sparrows selected nest shrubs and nest niches within shrubs that were warmer and less variable compared with unused but available sites (Table 3). Sagebrush Sparrows also selected shrubs that were warmer with less temperature variation than unused sites, and tended to select warmer and less variable nest niches (Table 3). We found no systematic differences in temperature between used and unused nest sites in Sage Thrashers at either the nest shrub or niche scale (Table 3).

**Other Factors Associated with Selection for Temperature**

**Brewer’s Sparrows.** Nest-site selection on the basis of temperature for Brewer’s Sparrows was invariant with our proxy of nest predation risk (Table 4). When temperatures were warmer during the nest-site prospecting period, Brewer’s Sparrows dampened selection for warmer nest sites at both the shrub (β = 0.02, 95% CI: −0.01 to 0.10; R² = 0.11) and nest-niche (β = 0.07, 95% CI: 0.02–0.12, R² = 0.10) scale (Table 4, Figure 3). The null model was the top model for temperature variability during prospecting at both spatial scales (Table 4).

**Sagebrush Sparrows.** Nest-site selection on the basis of temperature at both spatial scales for Sagebrush Sparrows was not influenced by our proxy of nest predation risk or ambient temperatures during nest-site prospecting. The null model was the top-ranked model for average nest shrub and nest niche temperature and temperature variability relative to random sites (Table 4). Only the model including year ranked within ≤2 ΔAICc of the top model at the nest shrub scale in terms of temperature variability, and at the nest niche scale in terms of average temperature (Table 4).

**Sage Thrashers.** Nest-site selection on the basis of temperature for Sage Thrashers was invariant with our proxy of nest predation risk (Table 4). Sage thrashers tended to dampen selection for warmer nest sites compared with random sites at the nest shrub (β = 0.02, 95% CI: 0.001–0.09; R² = 0.06) and niche (β = 0.02, 95% CI: 0.001–0.09; R² = 0.07) scales when they experienced warmer ambient temperatures during the nest-site prospecting period (Table 4, Figure 4). Prospecting temperature variability did not influence temperature variability differences at preferred compared with random sites at either spatial scale (Table 4).

**DISCUSSION**

Extreme weather conditions pose risks to the viability of avian eggs, nestling survival, and attending parents. The
### TABLE 4

Competing AIC<sub>c</sub> models designed to assess whether nest predation risk or temperatures during nest-site prospecting influenced the nest-site selection of Brewer's Sparrows, Sagebrush Sparrows, and Sage Thrashers on the basis of temperature. All nests were located in 2017 and 2018 within or adjacent to the Jonah natural gas field and the Pinedale Anticline Project Area, Wyoming, USA. Surface disturbance served as an established proxy for the risk of nest predation. All models are reported and were fit with generalized linear mixed models with a gaussian distribution to allow a random intercept of study plot, with the difference in mean temperatures and temperature variance between used and unused nest sites (\(\text{Temperature}_{\text{used}} - \text{Temperature}_{\text{unused}}\)) as the response variables. Log(L) are the log-likelihood values, ΔAIC<sub>c</sub> is the difference in Akaike's information criterion (AIC<sub>c</sub>) values between the top-fitting model and the reported model, and \(w_i\) is the Akaike weight of each model representing fit.

| Species          | Scale                     | Model                                                                 | log(L)  | ΔAIC<sub>c</sub> | \(w_i\) |
|------------------|---------------------------|-----------------------------------------------------------------------|---------|------------------|---------|
| **Brewer's Sparrow** | **Nest shrub**           | Mean temperature                                                     | -107.49 | 0.00             | 0.32    |
|                  |                           | Intercept                                                             | -109.73 | 0.07             | 0.31    |
|                  |                           | Year                                                                  | -109.07 | 0.94             | 0.20    |
|                  |                           | Ambient + Surface disturbance + Year                                  | -107.40 | 2.08             | 0.11    |
|                  |                           | Surface disturbance + Year                                            | -109.04 | 3.09             | 0.07    |
|                  | Temperature variance      | Intercept                                                             | -396.44 | 0.00             | 0.55    |
|                  |                           | Year                                                                  | -396.36 | 2.02             | 0.20    |
|                  |                           | Surface disturbance + Year                                            | -395.68 | 2.87             | 0.13    |
|                  |                           | Ambient variance + Year                                              | -396.21 | 3.93             | 0.08    |
|                  |                           | Ambient variance + Surface disturbance + Year                         | -395.55 | 4.89             | 0.05    |
| **Nest niche**   | Mean temperature          | Ambient                                                               | -84.96  | 0.00             | 0.58    |
|                  |                           | Ambient + Surface disturbance + Year                                  | -84.49  | 1.36             | 0.29    |
|                  |                           | Intercept                                                             | -89.05  | 3.76             | 0.09    |
|                  |                           | Year                                                                  | -89.01  | 5.85             | 0.03    |
|                  |                           | Surface disturbance                                                   | -88.94  | 7.97             | 0.01    |
|                  | Temperature variance      | Intercept                                                             | -350.69 | 0.00             | 0.60    |
|                  |                           | Year                                                                  | -350.68 | 2.18             | 0.20    |
|                  |                           | Surface disturbance + Year                                            | -350.32 | 3.70             | 0.09    |
|                  |                           | Ambient variance + Year                                              | -350.58 | 4.21             | 0.07    |
|                  |                           | Ambient variance + Surface disturbance + Year                         | -350.25 | 5.86             | 0.03    |
| **Sagebrush Sparrow** | **Nest shrub**           | Mean temperature                                                     | -81.80  | 0.00             | 0.60    |
|                  |                           | Year                                                                  | -81.73  | 2.10             | 0.21    |
|                  |                           | Ambient + Year                                                       | -81.53  | 3.98             | 0.08    |
|                  |                           | Surface disturbance + Year                                            | -81.54  | 4.01             | 0.08    |
|                  |                           | Ambient + Surface disturbance + Year                                  | -81.27  | 5.85             | 0.03    |
|                  | Temperature variance      | Intercept                                                             | -291.29 | 0.00             | 0.53    |
|                  |                           | Year                                                                  | -291.02 | 1.69             | 0.23    |
|                  |                           | Surface disturbance + Year                                            | -290.45 | 2.84             | 0.13    |
|                  |                           | Ambient variance + Year                                              | -290.99 | 3.93             | 0.07    |
|                  |                           | Ambient variance + Surface disturbance + Year                         | -290.85 | 5.15             | 0.04    |
| **Nest niche**   | Mean temperature          | Intercept                                                             | -70.33  | 0.00             | 0.47    |
|                  |                           | Year                                                                  | -69.85  | 1.30             | 0.25    |
|                  |                           | Surface disturbance + Year                                            | -69.20  | 2.34             | 0.15    |
|                  |                           | Ambient + Year                                                       | -69.77  | 3.47             | 0.08    |
|                  | Temperature variance      | Intercept                                                             | -259.93 | 0.00             | 0.54    |
|                  |                           | Year                                                                  | -259.91 | 2.23             | 0.18    |
|                  |                           | Surface disturbance + Year                                            | -259.00 | 2.75             | 0.14    |
|                  |                           | Ambient variance + Year                                              | -259.54 | 3.84             | 0.08    |
|                  |                           | Ambient variance + Surface disturbance + Year                         | -258.59 | 4.35             | 0.06    |
| **Sage Thrasher** | **Nest shrub**           | Mean temperature                                                     | -80.93  | 0.00             | 0.38    |
|                  |                           | Ambient + Year                                                       | -78.75  | 0.21             | 0.34    |
|                  |                           | Year                                                                  | -80.90  | 2.20             | 0.34    |
|                  |                           | Ambient + Surface disturbance + Year                                  | -78.70  | 2.50             | 0.13    |
|                  |                          Surface disturbance + Year                           | -80.87  | 4.46             | 0.04    |
TABLE 4. Continued

| Species | Scale     | Model                              | log(L)  | ΔAICc | wi |
|---------|-----------|------------------------------------|---------|-------|----|
|         | Temperature variance | Intercept | −291.98 | 0.00  | 0.52 |
|          |           | Year | −291.59 | 1.47  | 0.25 |
|          |           | Ambient variance + Year | −291.19 | 2.98  | 0.12 |
|          |           | Surface disturbance + Year | −291.58 | 3.76  | 0.08 |
|          |           | Ambient variance + Surface disturbance + Year | −291.18 | 5.37  | 0.04 |
| Nest niche | Mean temperature | Intercept | −65.93 | 0.00  | 0.39 |
|          |           | Ambient + Year | −63.78 | 0.36  | 0.33 |
|          |           | Year | −65.93 | 2.28  | 0.13 |
|          |           | Ambient + Surface disturbance + Year | −63.66 | 2.58  | 0.11 |
|          |           | Surface disturbance + Year | −65.76 | 4.32  | 0.05 |
|          |           | Intercept | −245.09 | 0.00  | 0.49 |
|          |           | Year | −244.81 | 1.74  | 0.21 |
|          |           | Ambient variance + Year | −243.81 | 2.13  | 0.17 |
|          |           | Surface disturbance + Year | −244.70 | 3.91  | 0.07 |
|          |           | Ambient variance + Surface disturbance + Year | −243.67 | 4.31  | 0.06 |

**FIGURE 3.** Effect of prospecting temperatures on mean temperature differences at used versus unused nest-sites (Temperature\_used - Temperature\_unused, wherein positive values indicate selection for a cooler nest site than unused but available sites and vice versa) for Brewer’s Sparrows at the shrub (top) and nest niche (bottom) scales. Results are based on model-averaged prediction outputs from a GLMM. Data were collected on the Jonah gas field and Pinedale Anticline Project Area south of Pinedale, Wyoming, USA during 2017 and 2018.

**FIGURE 4.** Effect of ambient temperature during the nest-site prospecting period on mean temperature differences at used and available nest-sites (Temperature\_used - Temperature\_unused, wherein positive values indicate selection for a cooler nest site than unused but available sites and vice versa) for Sage Thrashers at the shrub scale (top) and nest niche scale (bottom). Results are based on model averaged prediction outputs from a GLMM. Data were collected on and adjacent to the Jonah gas field and Pinedale Anticline Project Area south of Pinedale, Wyoming, USA during 2017 and 2018.
selection of nest sites is one potentially plastic behavior by which parents may be able to modulate such risks. Temperature, in particular, can exert both direct and indirect effects on the altricial young of passerines, and therefore should influence the selection of nest sites (Webb 1987, Visser 1998, Dawson et al. 2005, Fairhurst et al. 2012). Nesting in sites with lower temperature variation also can be energetically beneficial, given that parents must behaviorally regulate egg and nestling temperatures (Ardia et al. 2009, Robertson 2009, Auer and Martin 2017). Our results suggest that sagebrush songbirds selected nest sites as a function of temperature at two different spatial scales (nest shrub and nest niche), to varying extents across contexts, including species and ambient conditions.

Developing an understanding of the habitat characteristics that most affect microclimatic conditions at nests can inform management prescriptions for at risk-species within the context of a changing climate. The characteristics that most influenced average temperatures at nests for the two smaller birds, Brewer’s Sparrows and Sagebrush Sparrows, was the density of sagebrush shrubs within the surrounding patch. Increased shrub density was associated with cooler nest temperatures on average, especially later in the nesting season. For Sagebrush Sparrows, moreover, increased overhead cover and vigor of the nest shrub tended to dampen temperature variability at nests. For Sage Thrashers, however, average temperatures at nest sites decreased with proximity to the shrub edge and decreased side cover, especially during the early season when nests tended to be placed lower to the ground. The microhabitat factors influencing temperature variability at thrasher nests were less clear, however, with 4 models within 2 ΔAICc. Moreover, the intercept model ranked within 2 ΔAICc for both Brewer’s Sparrows and Sage Thrashers for habitat factors affecting temperature variance. We therefore cannot rule out the possibility that other habitat characteristics that we did not include may be important for nest microclimates. For example, the depth of the nest cups of Sage Thrashers appeared quite variable (T. Scherr, personal observation). Deeper nest cups, especially for larger songbirds such as Sage Thrashers, could provide thermal benefits via the regulation of surrounding air convection. Moreover, future investigations that explicitly examined whether the microhabitat characteristics preferred by parent songbirds are the same ones that most modulate temperatures at nests would further clarify relationships between nest-site preferences and different selective pressures.

Some of the differences in nest-site selection in relation to temperature we observed across species may be attributable to variation in body size. Smaller-bodied animals have a higher surface-area to volume ratio, enabling greater dispersal of body heat than larger-bodied birds. Yet, because songbirds usually remain on the nest throughout the night, the low nocturnal temperatures may be more energetically expensive for smaller than larger-bodied birds (Riesenfeld 1981). Indeed, cold extremes in many systems tend to drive patterns of thermal-tolerance in many avian species across latitudes (Stager et al. 2016, Pollock et al. 2019). The patterns we document corroborate this idea, as the two smaller sparrows tended to select warmer sites at both the nest niche and shrub scales whereas the largest species did not. In accordance with our predictions, moreover, both sparrows selected nest sites with dampened temperature variation. Organisms within open, high-elevation systems such as the sagebrush steppe often are exposed to highly variable temperatures, with nests in our system reaching temperatures as high as 50°C and as low as –5°C within a nesting period. Given the potential for such extreme conditions, there may be selection on small-bodied songbirds to limit the need to rapidly shed and gain heat to maintain the tight range of temperatures necessary for development of young.

Patterns of nest-site selection in relation to temperature were context-dependent for Brewer’s Sparrows and Sage Thrashers. Brewer’s Sparrows and thrashers dampened selection for warmer nest sites in comparison to unused but available sites when ambient temperatures were higher during the nest-site prospecting period. Sagebrush songbirds may therefore be able to proximately assess ambient temperature conditions and adjust nest-site selection accordingly. Trade-offs also may exist between nest-site selection for predation risk and microclimate (Rauter et al. 2002, Amat and Masero 2004, Forstmeier and Weiss 2004, Tieleman et al. 2008), though we did not observe selection for temperature vary along our established gradient of nest predation risk (Hethcoat and Chalfoun 2015a, b). The extent to which sagebrush-obligate songbirds can assess the risk of nest predation upon arrival at breeding sites in the spring is not fully understood, though the complexity of assessing the abundance and activity of a diverse suite of potential nest predators renders this possibility unlikely (Chalfoun and Martin 2010b). By contrast, temperatures experienced during the prospecting period likely provide more reliable information than nest predation risk on which to base nest-site choices.

Our study suggests that nest-site selection provides a behavioral mechanism by which songbird parents can buffer altricial offspring from temperature extremes. Future examinations of marked individuals across multiple nesting attempts and a range of temperature conditions would clarify the extent to which such behaviors represent behavioral plasticity. Regardless, the patterns we document have implications for the ability of small birds breeding in temperate zones to cope with temperature regimes as weather patterns continue to become more extreme and variable. The extent to which such buffering will be possible into the future will likely depend on the rate and extent of on-going climatic change. Moreover, although the
3 species of sagebrush-obligate songbirds that we studied herein are frequently considered together in management and risk assessments, our study demonstrated species-specific patterns of nest-site selection in relation to temperature metrics and the microhabitat characteristics most associated with temperatures at nests. These results underscore the importance of species-specific management prescriptions for nongame species when possible. Furthermore, the variable patterns of nest-site selection and microhabitats at nest sites that most influenced nest microclimates we observed across species highlights the importance of maintaining microhabitat heterogeneity within sagebrush (and other) landscapes, and patches of relatively high densities of mature shrubs with high vigor.

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Author contributions: Both authors conceived the idea, design, and experiment. T.M.S. collected the data and performed the research. T.M.S. analyzed the data and wrote the paper, with substantial input and edits from A.D.C. throughout. A.D.C. contributed substantial materials, resources, and funding.

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