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## Weather explains differences in sagebrush-obligate songbird nest success under various grazing regimes

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## ABSTRACT

Livestock grazing occurs worldwide, spanning over 25% of land globally, and effective conservation of biodiversity relies upon understanding the interactions of agricultural management practices and increasingly variable weather associated with climate change. We evaluated precipitation and temperature and the daily nest survival rates of two species of sagebrush-obligate songbirds, Brewer's sparrow (*Spizella breweri*) and sagebrush sparrow (*Artemisiospiza nevadensis*) under dormant season grazing, rotational grazing and a non-grazed control. Precipitation and temperature were quantified as daily time-varying and averages across the breeding season. Both sparrow species in our study were influenced by within-year weather variation, and experienced declines in daily nest survival beyond precipitation thresholds. For sagebrush sparrows, an interaction of precipitation and temperature indicated nest survival was lowest during 5-day time frames with minimal precipitation and high temperatures. While we found moderate grazing lowered perennial grass cover, there was no support for vegetation differences associated with moderate grazing explaining daily nest survival. Our results indicate that variable weather presented a much greater threat to these birds than reductions in herbaceous cover caused by moderate grazing under the studied conditions. Management should focus on conserving extensive tracts of suitable habitat to increase songbird populations and resiliency to increasingly variable and extreme weather conditions.

### 1. Introduction

Effective conservation of biodiversity relies upon understanding how working landscapes affect wildlife populations (Dirzo et al., 2014; König et al., 2020; Vitousek et al., 1997). Given the increasing demand for multiple land-uses, particularly for agricultural lands, understanding the interactions of management practices and natural sources of variation in population dynamics can help guide management and conservation (Hovick et al., 2015). For example, grazing covers at least 25% of global land surface and occurs across most biomes, particularly grasslands, open woodlands, deserts and sagebrush ecosystems (Asner et al., 2004). Livestock grazing has

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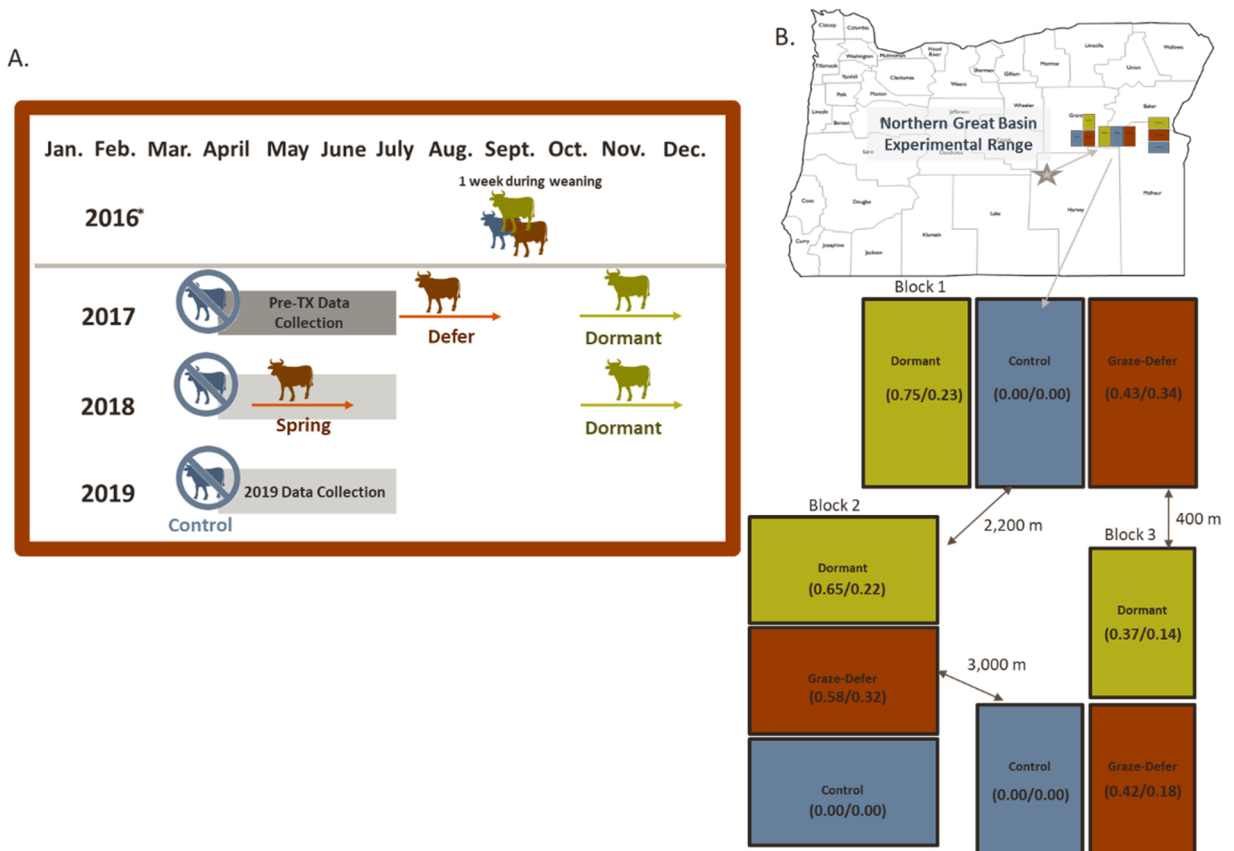
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been hypothesized to play an important role in wildlife population dynamics by altering plant community composition and structure (Beck and Mitchell, 2000), changing the distribution and abundance of nest predators (Bylo et al., 2014; Coates et al., 2016a; Johnson and Horn, 2008; Jones et al., 2003; Larson, 2014) or via direct interactions with cattle (Nack and Ribic, 2005).

Seasonal timing of grazing may lead to varying effects on songbirds. For example, grazing during the dormant season (late fall or winter during plant dormancy in the northern Great Basin) when birds are not breeding can eliminate direct interactions between cattle and songbirds. Yet both dormant and growing season grazing may alter available vegetative cover (Davies et al., 2018). This potentially influences screening cover for nesting (Yeo, 2005) or food resources for birds (Debano, 2006; Goosey et al., 2019; Kruess and Tschamtko, 2002) or some of their omnivorous predators (Torre et al., 2007). Higher grazing pressure during the growing season has been identified as a potential threat to sagebrush-obligate birds (Beck and Mitchell, 2000; Monroe et al., 2017). Moderate grazing regimes incorporating rest and rotation have not been associated with decreasing bird reproduction (Dettenmaier, 2018; Ruth, 2019; Smith et al., 2018a, 2018b). However, these studies were not designed to test rotational grazing versus no grazing; thus, did not have no-grazing controls. Furthermore, there is no research providing direct evidence that rotational grazing influences sagebrush-obligate bird reproduction.

While grazing effects on sagebrush-obligate songbird populations remain poorly quantified, weather effects are better understood. Weather might play the most significant role in determining reproductive success in sagebrush birds (Dinkins et al., 2016; Hightower et al., 2018; Petersen et al., 1986; Rotenberry and Wiens, 1991; Smith et al., 2018a; Webb et al., 2012). High daily maximum temperatures can reduce sagebrush sparrow growth rates, potentially through heat stress or by impairing adults' foraging ability (Petersen et al., 1986). Severe weather, such as unseasonably cold and wet or hot and dry periods, might exert bottom-up effects by reducing food availability, potentially delaying fledging which lowers recruitment (Shutler et al., 2006), reducing nestling growth rates (Wright et al., 1998) or increasing nestling mortality rates (Zanette et al., 2006). The expectation of more extreme high temperatures, greater



**Fig. 1.** A) Timeline of grazing treatment application and songbird daily nest survival collection. Grazing treatments represented by cow icons and include dormant season (green), rotational spring/summer graze (red orange) and non-grazed control (blue). Gray boxes represent nesting season data collection. The dark gray box represents pre-treatment nesting season data collection. Gray horizontal line separates pre-study time frame. \*2016 grazing prior to study establishment included one week of grazing during weaning in blocks 1–2 across all treatment sites and no grazing in block 3. B) Study site layout of randomized experimental block design, consisting of 3 blocks, each with 1 site of each treatment. Double sided arrows indicate closest distance from fence to fence within blocks. Study located at the Northern Great Basin Experimental Range (NGBER) in southeast Oregon, USA. Data presented only for 2017–2019 breeding seasons. Treatments were randomly assigned. Site size varied among, but not within, blocks (5.69–7.41 HA). Animal Unit Months per Hectare are reported within the parentheses for each site for 2017 and 2018, respectively.

precipitation intensity, and variability in summer temperatures due to climate change (Almazroui et al., 2021; Meehl et al., 2016) heightens the need for information regarding effects of weather on sagebrush-obligate songbirds as well as potential interactive effects with grazing.

Replicated experiments with controls and pre-treatment data evaluating the effects of grazing on wildlife are nearly non-existent in the current literature. We evaluated grazing and weather interactions within a replicated grazing experiment testing different grazing seasons of use versus non-grazed controls in the sagebrush ecosystem of southeastern Oregon. We studied the influence of two key weather variables, temperature and precipitation, on the nest success rates of two species of sagebrush-obligate songbirds, Brewer's sparrow (*Spizella breweri*) and sagebrush sparrow (*Artemisiospiza nevadensis*). We hypothesized that weather would be an important factor in determining nest success. Furthermore, we hypothesized that grazing could lead to differences in nest success, potentially through decreased herbaceous nesting cover, food resources or altered predator-prey dynamics, but would have a lesser influence on Brewer's sparrows, which nest off the ground in shrubs, than sagebrush sparrows, which nest closer to the ground.

## 2. Methods

### 2.1. Study area

We conducted our study within the Northern Great Basin Experimental Range (NGBER; lat 43°29'N, long 119°43'W) 50–60 km west of Burns, Oregon, USA, from 2017 to 2019. Elevation of the sites ranged from 1300–1500 m. Climate was typical of the northern Great Basin, and consisted of wet, cool winters followed by hot, dry summers with a long-term (1938–2015) average crop year precipitation of 278 mm (NOAA station, Riley 10 WSW, OR US). Precipitation during the study years was 107% (2017), 66% (2018), and 130% (2019) of the long-term average.

All treatments within blocks experienced the same historical grazing regime, had similar plant communities, soils, aspect and gradients prior to treatment. Prior to the study, grazing was consistent within but not across blocks. In 2016 and 2015 (1 and 2 years prior to study initiation), blocks 1 and 2 were grazed for one week in September during weaning (Fig. 1). Block 3 was grazed for one month in the spring in 2015 and no grazing occurred in block 3 in 2016. All sites within a block experienced the same historical grazing, as blocks were created by subdividing an existing established pasture into three smaller study sites. Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and green rabbitbrush (*Chrysothamnus viscidiflorus*) were the dominant shrubs. Dominant grasses included bluebunch wheatgrass (*Pseudoroegneria spicata*), Thurber's needlegrass (*Achnatherum thurberianum*), bottlebrush squirreltail (*Elymus elymoides*), Idaho fescue (*Festuca idahoensis*), prairie junegrass (*Koeleria macrantha*), and needle and thread (*Hesperostipa comata*). Site plant communities were representative of those in the northern Great Basin (Davies et al., 2006; Davies and Bates, 2010) dominated by native perennial species, and exhibited minimal invasion by exotic annual grasses.

### 2.2. Study design and grazing treatment application

We used a before-after-control-impact (BACI) randomized complete block design within nine sites (5.69–7.41 ha) arranged into three blocks, each consisting of three randomly assigned grazing treatments, to determine the effects of grazing on sagebrush-obligate songbird daily nest survival (Fig. 1). Grazing treatments consisted of dormant season grazing, rotational (alternating spring then summer) grazing and non-grazed controls. Site size varied among, but not within blocks. Pre-treatment data collection occurred during the 2017 breeding season prior to any grazing treatment application, while 2018 and 2019 reflect post-treatment nest-survival. Dormant season grazing treatment occurred during fall or winter of 2017–2018, after the native bunchgrasses entered dormancy. The rotational grazing treatment consisted of alternating between summer grazing after bunchgrasses completed reproduction (~mid-July 2017) and spring growing season grazing during May (2018; Fig. 1).

Herbaceous forage production varied across space (blocks and sites) and through time (year and season). In practice, using a consistent stocking rate throughout sites and years would have resulted in variable grazing intensities due to differences in available forage. Therefore, we varied stocking rates by herbaceous forage amount, quantified by systematically clipping herbaceous material in 15, 1 m<sup>2</sup> quadrats throughout each site once immediately prior to grazing, in order to achieve moderate grazing utilization (Bates and Davies, 2014). We then visually assessed sites during cattle grazing to prevent over or under-utilization. A resource management professional of the local Bureau of Land Management (BLM) helped assess the post-treatment level of grazing utilization using BLM landscape appearance protocols (Coulloudon et al., 1999). Animal unit months per hectare varied by site and herbaceous amount available, with 2017 having greater production and higher stocking rates (rotational: 0.42–0.58, dormant: 0.37–0.75) to reach moderate grazing compared to 2018 (rotational: 0.18–0.34, dormant: 0.14–0.23, Fig. 1).

### 2.3. Field methods

#### 2.3.1. Nest searching

We found nests of Brewer's sparrow and sagebrush sparrow by systematically searching each site during April–July with sites searched weekly. We found nests through the combination of behavioral cues and systematic searches, where researchers walked transects 5 m apart, lightly tapping shrubs with a 2 m long flush stick, and intensively searching shrubs when songbirds flushed.

#### 2.3.2. Nest monitoring

We monitored nests every 1–4 days until fate, with most nests experiencing <72 h between nest checks (Chalfoun and Martin,

2010; Hethcoat and Chalfoun, 2015a; Martin and Geupel, 1993). We defined success as nests which produced at least one fledgling, determined by the presence of fledglings near the nest, adults alarm calling or carrying food items nearby, or the nest bowl condition and evidence that chicks were fledging age (Chalfoun and Martin, 2010; Manolis et al., 2000; Martin and Geupel, 1993). We deemed nests unsuccessful if we documented a depredation event or the disappearance of eggs or chicks before fledging age (Chalfoun and Martin, 2010; Manolis et al., 2000). To aid in accurate determination of daily nest survival, we utilized trail cameras (Cuddeback Black Flash [Silver Series], Model 1231) and iButton temperature loggers (model DS1921GF5) at a subset ( $n = 101$ ,  $n = 7$ , respectively) of nests. Paired iButtons helped us identify an empty or abandoned nest when a nest iButton expressed a similar temperature profile to an iButton located outside the nest within that nesting shrub, indicating an empty nest or cessation of parental care (Hartman and Oring, 2006; Sutti and Strong, 2014). Cameras were well camouflaged and placed 20–150 cm away from nests either within the nesting shrub or in an adjacent shrub that optimized the viewshed while minimizing disturbance (Hethcoat and Chalfoun, 2015b).

### 2.3.3. Vegetation sampling

We measured site-level vegetation cover and density along 12, 50 m transects evenly spaced throughout the study sites. Herbaceous canopy cover was measured by using the line-point-intercept method (Herrick et al., 2009). We recorded vegetation cover every 1 m by dropping a pin along transects and recorded every plant (species level for grasses and shrubs, and functional group for forbs [invasive annual forb, native annual forb, invasive perennial forb, or native perennial forb]). Density of perennial herbaceous species was determined by counting all plants rooted within 0.25 m<sup>2</sup> quadrats placed at three-meter intervals for a total of 15 quadrats per transect. We used the line-intercept technique to quantify shrub canopy cover by species (Canfield, 1941), and we measured shrub density by counting all individuals rooted inside 2 × 50 m belt transects.

We characterized nest shrub-level vegetation metrics within 3 days of estimated fledge date (instead of at fate-date) to avoid temporal bias where successful nests are measured later in the season, thus confounded with plant phenology of vegetation at and near nests (e.g., Smith et al., 2018c). Furthermore, at each nest shrub, we only recorded vegetation metrics not expected to change on short time scales, including shrub species, shrub height (excluding inflorescence), nest rim height within the shrub and percent alive (estimated ocularly from 0% to 100%). Nest shrub canopy area was measured as the longest diameter of the shrub and the length of the perpendicular diameter, then calculating area as an ellipse. To characterize the nest placement within the shrub, we recorded the orientation of the nest relative to the shrub stem, measured in degrees from north, and recorded the height of shrub directly above the nest.

## 2.4. Weather data

We obtained weather data from a nearby National Oceanic and Atmospheric Administration station (Riley 10 WSW, OR US; 43.4711°, -119.6917°). The weather station was 1 km from the closest site and 2.5 km from the farthest, and generally captured all weather events experienced by all study sites. We assessed temperature and precipitation variables for two timeframes: breeding season and daily time-varying (aligning weather with each day the nest was active, while also including different lengths of time before each day [ $t$ ]) variables within the nesting season (Table A1). Within season weather variables included daily, 5-day and 10-day time-varying weather. In addition to daily weather, we summarized temperature (average) and precipitation (cumulative) as 5-day ( $t, t-1 \dots t-4$ ) and 10-day ( $t, t-1 \dots t-9$ ) moving windows to assess the cumulative effect of weather over roughly a quarter (5-day) and half (10-day) of the nesting timeframe of the songbirds (Brewer's sparrow: average incubation 10–12 days, nestlings 7–10 days; sagebrush sparrow: average incubation 10–16 days, nestlings 9–10 days). We did not assess longer timeframes to avoid including days unlikely to have influenced adults as they were nest building, laying eggs and incubating their nests (Martin and Carlson, 2020; Rotenberry et al., 2020). In addition, second nests initiate on average 10 days after fledging of a previous nest (Green, 1981; Martin and Carlson, 2020; Rotenberry et al., 2020).

## 2.5. Analyses

All daily nest survival analyses were done using the logistic exposure method (Shaffer, 2004). Logistic exposure utilizes an encounter history to model daily nest survival as a logistic function of the explanatory variables over the timeframe the nest was active. This method accounts for possible bias imposed by nests with different exposure periods found after nest initiation. We estimated overall nest success independent of all covariates using Mayfield's method (Mayfield, 1975). To analyze daily nest survival using the logistic exposure method for each species we used generalized linear mixed models (GLMM, glmer function in package lme4) with block as a random effect in program R (x64 version 3.6.1).

We modelled daily nest survival separately for Brewer's sparrow and sagebrush sparrow, using an information-theoretic approach (Anderson, 2007). We conducted a combination of predictive modelling and hypothesis testing modelling by first developing a predictive model that we then used to test our grazing hypotheses. Models were compared using Akaike's Information Criterion corrected for small sample sizes (AIC<sub>c</sub>) and Akaike model weights ( $w_i$ ; Akaike, 1987, 1973; Burnham and Anderson, 2002) using the AICcmodavg package in R (Mazerolle, 2020).

### 2.5.1. Predictive modelling

To develop the predictive model, we divided variables into three covariate sets: weather (temperature and precipitation quantified as season long or daily time-varying), camera/iButton, and vegetation (at nest and site-level, Table A1). We evaluated each of the three covariate sets in two steps: (1) as individual, quadratic covariates and pair-wise interactive terms and (2) as additive combinations

from step 1. In step 1, we followed [Arnold's \(2010\)](#) approach for eliminating uninformative parameters by removing non-informative covariates from single covariate models defined as those with parameter estimate 85% confidence intervals (CIs) that overlapped zero. In step 2, we tested and ranked models, using  $\Delta AIC_c$ , additive combinations of all remaining informative predictor variables (single, quadratic or pairwise interactions). We did not include any two predictor variables with Pearson's correlation coefficient  $r \geq |0.65|$  in additive models to avoid multicollinearity and retained the best fitted variable as ranked by  $\Delta AIC_c$  when correlation occurred. We then considered models within two  $\Delta AIC_c$  of the top overall model competitive ([Burnham and Anderson, 2002](#)). In step 2 of the weather covariate set, we assessed day of nesting season as a single variable to compare with our weather models.

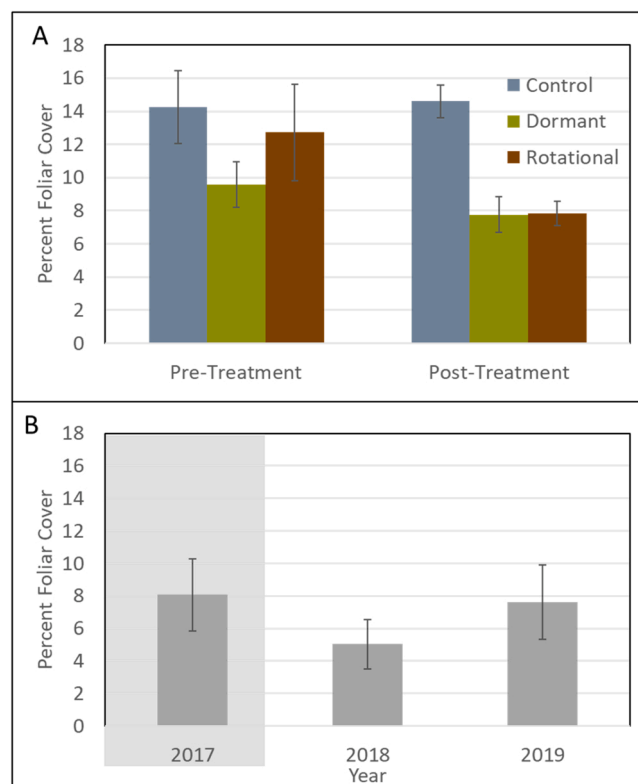
We advanced all competitive models from each covariate set to the next modelling step, creating the full predictive model. To determine the best predictive model, we tested and ranked, using  $\Delta AIC_c$ , additive combinations of all competitive models from the three covariate sets. All competitive models from the full predictive modelling step were advanced to grazing hypothesis testing.

### 2.5.2. Grazing hypothesis testing

We utilized the predictive model(s) to evaluate our a priori grazing hypotheses by comparing the additive and multiplicative combinations of two different categorical grazing treatment site variables (dormant, rotational spring/summer and control [treatment type] and grazed versus non-grazed) and time. Time was evaluated as pre-treatment (2017 breeding season) versus post-treatment (2018 and 2019 breeding seasons) based on our BACI design ([Fig. 1](#)). We discuss results and inferences for competitive models and the models specifically testing our grazing hypothesis (treatment sites x pre/post and/or grazed sites x pre/post).

### 2.5.3. Vegetation

We analyzed the influence of grazing treatment on herbaceous cover (perennial bunchgrasses and forbs) using the lmer function in package lme4 ranking models using  $AIC_c$  and  $w_i$ . Fixed variables included treatment, year and pre-treatment (2017 breeding season) versus post-treatment (2018 and 2019 breeding seasons). We also evaluated interactions between treatment x year and treatment x pre/post. Block was included as a random variable. Vegetation figures present original (i.e., non-modelled) data, and error bars represent 85% CI.



**Fig. 2.** Perennial bunchgrass (A) and perennial forb (B) cover values (mean),  $n = 3$ , for 3 years of data collection (2017–2019) in grazing treatment sites (dormant season (green), rotational spring/summer graze (red orange) and non-grazed control (blue; [Fig. 1](#)) in southeast Oregon, USA. 2017 represents the pre-treatment year: cattle grazing had not yet been applied (indicated by gray box). Error bars represent 85% confidence intervals. Treatment  $\times$  PrePost interaction not shown for perennial forb cover (B) as it was not competitive with the top model ([Table A2](#)). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

### 3. Results

We monitored 230 total sagebrush-obligate songbird nests, including 132 sagebrush sparrow and 97 Brewer’s sparrow nests for a total of 1672 and 1181 cumulative exposure days, respectively. One nest was excluded from the analysis due to researcher-caused failure where a researcher led cattle directly to a nest upon which it was trampled. While we did not evaluate nest density, nest searching effort was similar across all treatments; thus, nest numbers likely approximate nest density. Number of discovered nests across treatment types for each species was 31, 31 and 35 Brewer’s sparrow nests and 41, 52 and 40 sagebrush sparrow nests in control, dormant and rotationally grazed plots, respectively. We attributed predation, abandonment, and parasitism as the causal factor for 77%, 22% and 1% of failed nests, respectively. Estimated Mayfield nest success of the entire study summarized by year for Brewer’s sparrow over an average incubation to fledging timeframe of 20 days was 0.65, 0.45 and 0.59, and 0.66, 0.59 and 0.31 for sagebrush sparrow over a 23-day average nesting timeframe for 2017, 2018 and 2019, respectively. No cameras or iButtons were placed on nests in 2017. During 2018 and 2019, cameras were placed on 12 of the Brewer’s sparrow nests in control, 11 nests in dormant and 13 nests found in rotationally grazed plots, while 16 sagebrush sparrow nests found in control received cameras, 22 nests found in dormant and 17 nests found in rotational sites. Herbaceous utilization from grazing averaged 50.1% (range: 28.0–61.1%) throughout the study.

#### 3.1. Vegetative cover

The top  $\Delta AIC_c$  selected model for perennial bunchgrass cover was treatment sites  $\times$  pre/post with  $w_i = 0.71$  (Table A2). Our treatment sites  $\times$  pre/post interaction indicated that our rotational grazing treatments reduced perennial bunchgrass cover after treatment (2018 and 2019 compared to 2017 parameter estimate =  $-4.12$ , 85% CI:  $-1.84, -2.77$ ; Fig. 2A). Perennial bunchgrass cover trended downward in dormant grazed sites, but the effect was not precise between pre- and post-treatment (parameter estimate =  $-1.37$ , 85% CI:  $-3.65, 0.91$ ; Fig. 2A). Year best explained differences in perennial forb cover, the treatment sites  $\times$  pre/post and treatment sites  $\times$  year interactions were not competitive with the top model, and the treatment sites only model did not outcompete the null (Table A2). Perennial forb cover was higher in 2017 (estimate =  $3.03$ , 85% CI:  $1.44, 4.63$ ) and 2019 (estimate =  $2.90$ , 85% CI:  $1.44, 4.36$ ).

**Table 1**

Logistic exposure nest success predictive models comparing weather, vegetation, camera/iButton variables as covariate sets and combined predictive model set among sites and years for Brewer’s sparrow (BRSP,  $n = 97$ ) in southeast Oregon, USA, 2017–2019. Block was included as a random effect in all models. K is the number of model parameters,  $\Delta AIC_c$  is the difference from the top model in Akaike’s Information Criterion adjusted for small sample size, and  $w_i$  is the model weight. See Table A1 for variable descriptions. Only the top 10 models above the null are displayed for brevity. <sup>2</sup> indicates a squared term. <sup>a</sup>AICc = 280.77, <sup>b</sup>AICc = 280.99, <sup>c</sup>AICc = 281.00, <sup>d</sup>AICc = 279.40, <sup>e</sup>AICc = 277.14.

Covariate set and model	K	$\Delta AIC_c$	$w_i$	Deviance
<b>Weather</b>				
Precip10day + Precip10day <sup>2</sup>	4	0.00 <sup>a</sup>	0.58	-136.37
1 (Null)	2	0.63	0.42	-138.69
<b>Camera/iButton</b>				
Camera	3	0.00 <sup>b</sup>	0.55	-137.49
1 (Null)	2	0.41	0.45	-138.69
<b>Vegetation</b>				
Perennial Forb Density	3	0.00 <sup>c</sup>	0.28	-137.49
Nest Height	3	0.05	0.27	-137.51
1 (Null)	2	0.40	0.23	-138.69
<b>Combined Predictive Model</b>				
(Precip10day + Precip10day <sup>2</sup> ) + Camera	5	0.00 <sup>d</sup>	0.15	-134.67
(Precip10day + Precip10day <sup>2</sup> ) + Camera + Nest Height	6	0.08	0.15	-133.7
(Precip10day + Precip10day <sup>2</sup> ) + Nest Height	5	0.64	0.11	-134.99
Precip10day + Precip10day <sup>2</sup>	4	1.38	0.08	-136.37
(Precip10day + Precip10day <sup>2</sup> ) + Perennial Forb Density + Camera	6	1.43	0.08	-134.38
Camera	3	1.59	0.07	-137.49
Perennial Forb Density	3	1.60	0.07	-137.49
Nest Height	3	1.65	0.07	-137.51
(Precip10day + Precip10day <sup>2</sup> ) + Camera + Perennial Forb Density + Nest Height	7	1.78	0.06	-133.54
(Precip10day + Precip10day <sup>2</sup> ) + Perennial Forb Density + Nest Height	6	1.93	0.06	-134.63
1 (Null)	2	2.00	0.06	-138.69
<b>Grazing Hypothesis Test</b>				
(Precip10day + Precip10day <sup>2</sup> ) + Camera + PrePost	6	0.00 <sup>e</sup>	0.08	-132.53
(Precip10day + Precip10day <sup>2</sup> ) + Camera + Nest Height + PrePost	7	0.59	0.06	-131.82
Camera + PrePost	4	0.80	0.06	-134.95
(Precip10day + Precip10day <sup>2</sup> ) + Camera + Grazed Sites + PrePost	7	1.22	0.05	-132.13
(Precip10day + Precip10day <sup>2</sup> ) + Camera + Perennial Forb Density + PrePost	7	1.56	0.04	-132.30
(Precip10day + Precip10day <sup>2</sup> ) + Camera + Nest Height + Grazed Sites + PrePost	8	1.76	0.03	-131.39
Camera + Grazed Sites + PrePost	5	1.91	0.03	-134.5
(Precip10day + Precip10day <sup>2</sup> ) + Camera + Nest Height+ Treatment Sites $\times$ PrePost	11	2.12	0.03	-128.52
(Precip10day + Precip10day <sup>2</sup> ) + Camera	5	2.26	0.03	-134.67
(Precip10day + Precip10day <sup>2</sup> ) + Camera + Treatment Sites $\times$ PrePost	10	2.28	0.03	-129.62
1 (Null)	2	4.26	0.01	-138.69

1.32, 4.51) compared to 2018 (Fig. 2B).

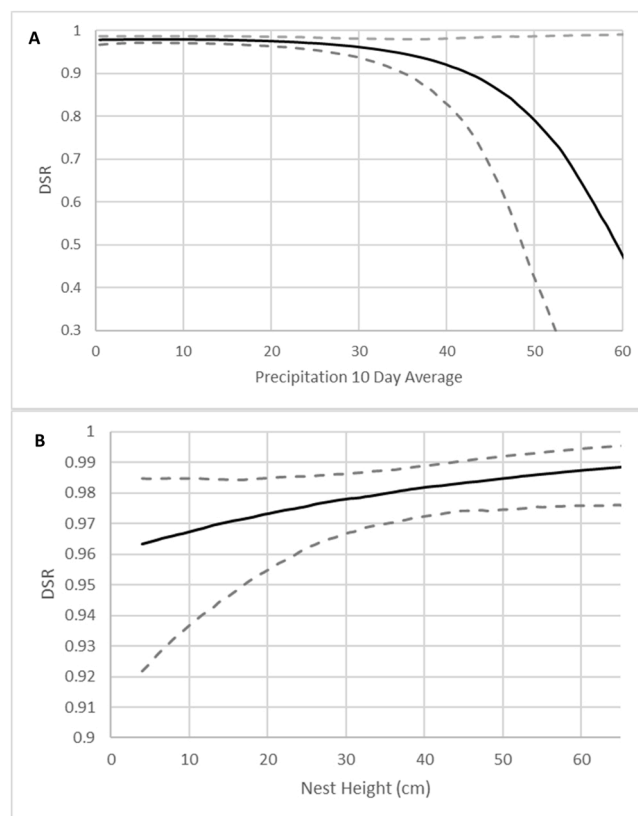
### 3.2. Brewer's sparrow

We found support for models predicting Brewer's sparrow DSR from the weather, camera/iButton and vegetation covariate sets (Table 1). Of the weather variables tested, only the quadratic relationship of time-varying precipitation calculated over 10 days, explained differences in DSR (Table 1). However, the null model was competitive with the top model ( $\Delta AIC_c = 0.63$  and  $w_i = 0.39$ ). For the vegetation and camera/iButton covariate sets, we found support for perennial forb density ( $w_i = 0.28$ ) and camera ( $w_i = 0.46$ ), respectively, although the null models ( $w_i = 0.23$  and  $w_i = 0.37$ , respectively) were also competitive (Table 1).

In the development of our predictive model, we found the most support for the model comprised of precipitation and camera variables (Table 1). However, this model only included 0.15 of the  $w_i$  and nine other models including various combinations of weather, vegetation, and camera were competitive (within  $2\Delta AIC_c$ ). Thus, we advanced all 10 competitive models from the predictive model set to the final model set, which tested our a priori grazing hypotheses. Seven models were considered competitive in the grazing hypothesis test model set. We found support for weather, camera, nest height, grazed versus treatment sites and the pre/post-treatment variables in the grazing hypothesis model set (Table 1). Perennial forb density and grazed site variables were not precise in any of the competitive models (parameter estimate had 85% CI overlap zero for all four models, Table 3). We report parameter estimates for all seven competitive models and the eighth  $\Delta AIC_c$ -ranked model, which directly assessed our grazing hypothesis (grazed sites  $\times$  pre/post; Tables 1 and 3).

Daily survival rate declined as time-varying precipitation across a 10-day timeframe increased, with more dramatic declines above 35 mm of precipitation (Fig. 3A). However, variability of this effect was high at the higher values of precipitation. DSR was lower in the post-treatment timeframe compared to pre-treatment timeframe regardless of treatment (Table 3). Birds that nested higher in shrubs had higher DSR, but nest height was only in two of the competitive models, and the parameter was slightly overlapping the 85% CI (Fig. 3B, Table 3).

We did not detect a precise effect of grazing treatment with our BACI design on Brewer's sparrow DSR as the interaction parameter estimates related to treatment sites  $\times$  pre/post were not precise (Tables 1 and 3). There was limited support suggesting a site effect



**Fig. 3.** Predicted effect of A) time-varying cumulative precipitation over ten-days and B) nest height from the ground to the nest rim on daily survival rate (DSR) of Brewer's sparrows in southeast Oregon, USA 2017–2019. Predictions shown for the top  $AIC_c$ -selected model of each variable (top model for A, second model for B) while holding all other predictor variables at their median values for continuous variables and post-treatment and camera for categorical variables, where applicable. Error bars represent 85% prediction intervals calculated using bootstrapping at 1000 iterations. See Table A1 for detailed variable descriptions.

where nests in dormant season sites had lower DSR compared to control sites across all years of the study (Tables 1 and 3). This site effect was not a treatment effect as the treatment effect (treatment sites × pre/post) was not competitive (Table 1). The rotational spring/defer grazing treatment variable was highly imprecise, and the dormant season grazing treatment variable trended towards a positive effect of dormant season grazing but was also imprecise at the 85% CI. Despite occurring in 3 of the competitive models, the grazed site effect was imprecise (Tables 1 and 3).

### 3.3. Sagebrush sparrow

We found that sagebrush sparrow DSR was best predicted by weather, vegetation and camera covariates within their respective covariate sets (Table 2). The interaction of time-varying average maximum temperature and time-varying cumulative precipitation, over a 5-day time frame, best explained differences in DSR (Table 2). Density of low sagebrush (*Artemisia arbuscula*) was ranked highest in the vegetation covariate set but did not markedly outperform the null model (0.65 ΔAIC<sub>c</sub> above the null model). Camera presence was the best model in the camera/iButton covariate model set with 4.05 ΔAIC<sub>c</sub> above the null model (Table 2).

Four models containing weather, vegetation and camera variables were competitive in the predictive model set, thus were advanced to the hypothesis testing step (Table 2). In our final modeling step, we found support for precipitation, temperature, camera, density of low sage, grazing site locations and the pre-treatment/post-treatment time frame variables (Tables 2 and 4). Five models were competitive in the hypothesis testing model step. We found support for both site and pre/post time effects regardless of treatment (Table 4). The second most supported model included the model assessing the grazing treatment effect (grazing site × pre-post-treatment; Table 2). However, this effect was imprecise (Table 4). Sites assigned grazing treatments had lower DSR regardless of time, and nests in all treatments had lower DSR in the post-treatment time frame compared to pre-treatment (Table 4).

**Table 2**

Logistic exposure nest success predictive models comparing weather, vegetation, researcher camera/iButton variables as covariate sets and combined predictive model set among sites and years for sagebrush sparrow (n = 132). Block was included as a random effect in all models. K is the number of model parameters, ΔAIC<sub>c</sub> is the difference from the top model in Akaike’s Information Criterion adjusted for small sample size, and w<sub>i</sub> is the model weight. See Table A1 for variable descriptions. Only the top 10 models above the null are displayed for brevity. Precip = precipitation. <sup>2</sup> indicates a squared term. <sup>a</sup>AICc = 394.75, <sup>b</sup>AICc = 416.17, <sup>c</sup>AICc = 41.7, <sup>d</sup>AICc = 391.35, <sup>e</sup>AICc = 387.30. Site is included as a random factor in all models. <sup>f</sup>weather = top model from weather covariate set: (Precip5day + Precip5day<sup>2</sup>) × MaxT\_5day.

Covariate set and model	K	ΔAIC <sub>c</sub>	w <sub>i</sub>	Deviance
<b>Weather</b>				
(Precip5day + Precip5day <sup>2</sup> ) × MaxT_5day	7	0.00 <sup>a</sup>	0.39	-190.34
Precip 5-day × MaxT_5day	5	0.88	0.25	-192.80
(Precip5day + Precip5day <sup>2</sup> ) × MaxT_5day+ Breeding Season Precip	8	0.98	0.24	-189.82
Precip5day × MaxT_5day + Breeding Season Precip	6	2.38	0.12	-192.54
Day of Nesting Season	3	18.18	0.00	-203.46
Breeding Season Precip	3	22.64	0.00	-205.69
1 (Null)	2	25.46	0.00	-208.11
<b>Vegetation</b>				
Low Sage Density	3	0.00 <sup>b</sup>	0.52	-207.03
1 (Null)	2	0.15	0.48	-208.11
<b>Camera/I-button</b>				
Camera	3	0.00 <sup>c</sup>	0.88	-205.08
1 (Null)	2	4.05	0.12	-208.11
<b>Combined Predictive Model</b>				
(Precip5day + Precip5day <sup>2</sup> ) × MaxT_5day+ Camera	8	0.00 <sup>d</sup>	0.24	-187.63
(Precip5day + Precip5day <sup>2</sup> ) × MaxT_5day+ Low Sage Density + Camera	9	0.17	0.22	-186.71
(Precip5day + Precip5day <sup>2</sup> ) × MaxT_5day+ Breeding Season Precip + Camera	9	1.66	0.10	-187.45
(Precip5day + Precip5day <sup>2</sup> ) × MaxT_5day+ Breeding Season Precip + Camera + Low Sage Density	10	1.81	0.10	-186.52
Precip 5-day × MaxT_5day+ Camera	6	2.10	0.08	-190.70
Precip 5-day × MaxT_5day+ Camera + Low Sage Density	7	2.17	0.08	-189.73
(Precip5day + Precip5day <sup>2</sup> ) × MaxT_5day	7	3.40	0.04	-190.34
(Precip5day + Precip5day <sup>2</sup> ) × MaxT_5day+ Low Sage Density	8	3.67	0.04	-189.47
Precip 5-day × MaxT_5day	5	4.28	0.03	-192.80
(Precip5day + Precip5day <sup>2</sup> ) × MaxT_5day+ Breeding Season Precip + Low Sage Density	8	4.38	0.03	-189.82
1 (Null)	2	28.87	0.00	-208.11
<b>Grazing Hypothesis Test</b>				
Weather <sup>f</sup> + Low Sage Density + Camera + Grazed Sites + PrePost	11	0.00 <sup>e</sup>	0.17	-182.57
Weather <sup>f</sup> + Low Sage Density + Camera + Grazed Sites × PrePost	12	1.08	0.10	-182.09
Weather <sup>f</sup> + Low Sage Density + Camera + Breeding Season Precip + Grazed Sites + PrePost	12	1.39	0.09	-182.46
Weather <sup>f</sup> + Low Sage Density + Camera + Treatment Sites + PrePost	12	1.81	0.07	-184.54
Weather <sup>f</sup> + Low Sage Density + Camera + Grazed Sites	10	1.91	0.07	-185.14
Weather <sup>f</sup> + Low Sage Density + Camera + Breeding Season Precip + Grazed Sites × PrePost	13	2.52	0.05	-185.26
Weather <sup>f</sup> + Low Sage Density + Camera + PrePost	10	3.11	0.04	-186.39
Weather <sup>f</sup> + Low Sage Density + Camera + Breeding Season Precip + Treatment Sites + PrePost	13	3.13	0.04	-184.41
Weather <sup>f</sup> + Camera + Grazed Sites + PrePost	10	3.36	0.03	-186.62
Weather <sup>f</sup> + Camera + PrePost	9	3.59	0.03	-187.63
1 (Null)	2	32.92	0.00	-208.11



**Table 3**

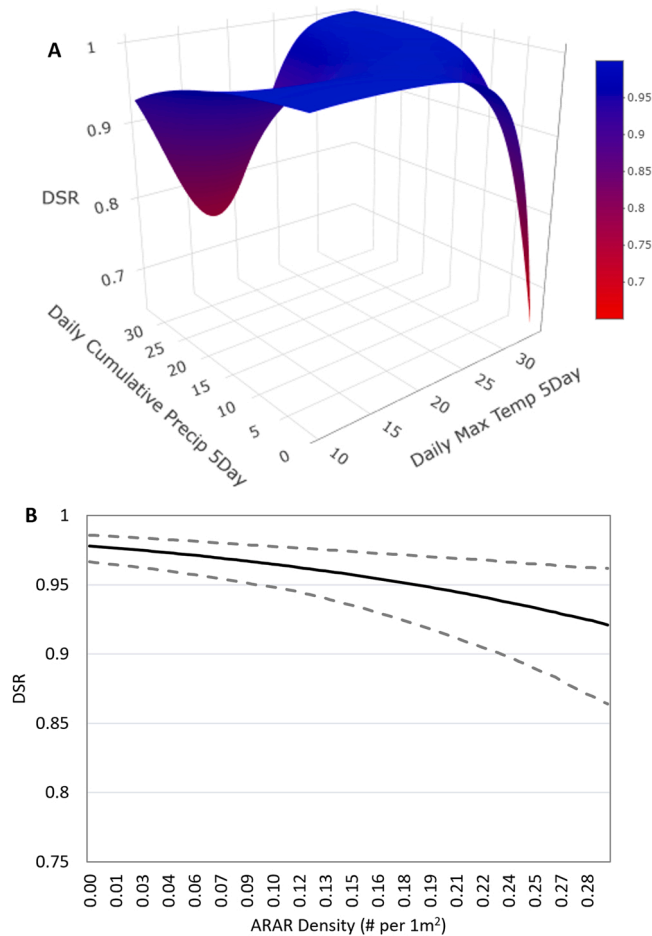
Parameter estimates with 85% confidence intervals (LCL and UCL) from top AICc-selected logistic exposure models for Brewer's sparrow (Table 2) in southeast Oregon, USA, 2017–2019. See Table A1 for a list of all tested covariates, their descriptions and summaries. Models listed in order of AICc ranking. Bold indicates 85% CI does not include zero, NA indicates parameter is not present in model and <sup>2</sup> indicates a squared term. <sup>a</sup> -0.001 (-0.0026, -0.0002), <sup>b</sup> -0.002 (-0.0028, -0.0003), <sup>c</sup> -0.001 (-0.0025, -0.0001), <sup>d</sup> -0.001 (-0.0025, 0.0000), <sup>e</sup> -0.001 (-0.0027, -0.0002), <sup>f</sup> -0.002 (-0.0029, -0.0003), <sup>g</sup> 0.02 (-0.004, 0.043), <sup>h</sup> 0.03 (0.001, 0.05).

Parameter estimates (85% CI)								
Parameter name	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8
Intercept	<b>3.60 (3.09, 4.12)</b>	<b>2.93 (1.99, 3.87)</b>	<b>3.63 (3.17, 4.09)</b>	<b>3.88 (3.19, 4.56)</b>	<b>3.78 (3.15, 4.41)</b>	<b>3.20 (2.16, 4.23)</b>	<b>3.91 (3.27, 4.54)</b>	<b>3.50 (1.80, 5.21)</b>
Precip10day	0.02 (-0.03, 0.07)	0.03 (-0.02, 0.08)	NA	0.02 (-0.03, 0.07)	0.02 (-0.03, 0.07)	0.03 (-0.03, 0.08)	NA	0.03 (-0.02, 0.09)
Precip10day <sup>2</sup>	<sup>a</sup> <b>0.00 (0.00, 0.00)</b>	<sup>b</sup> <b>0.00 (0.00, 0.00)</b>	NA	<sup>c</sup> <b>0.00 (0.00, 0.00)</b>	<sup>d</sup> 0.00 (0.00, 0.00)	<sup>e</sup> <b>0.00 (0.00, 0.00)</b>	NA	<sup>f</sup> <b>0.00 (0.00, 0.00)</b>
Camera Present	<b>1.04 (0.48, 1.60)</b>	<b>0.95 (0.38, 1.52)</b>	<b>0.97 (0.43, 1.50)</b>	<b>1.04 (0.48, 1.60)</b>	<b>0.99 (0.42, 1.56)</b>	<b>0.96 (0.39, 1.53)</b>	<b>0.96 (0.42, 1.50)</b>	<b>0.93 (0.36, 1.51)</b>
PrePost: Post Treatment	-0.84 (-1.44, -0.25)	-0.80 (-1.40, -0.20)	-0.91 (-1.50, -0.32)	-0.89 (-1.49, -0.29)	-0.83 (-1.43, -0.23)	-0.85 (-1.46, -0.25)	-0.96 (-1.56, -0.36)	-1.42 (-2.97, 0.12)
Nest Height	NA	<sup>g</sup> 0.02 (0.00, 0.04)	NA	NA	NA	<sup>g</sup> 0.02 (0.00, 0.04)	NA	<sup>h</sup> <b>0.03 (0.00, 0.05)</b>
Grazed Sites	NA	NA	NA	-0.32 (-0.85, 0.20)	NA	-0.33 (-0.86, 0.20)	-0.34 (-0.86, 0.18)	NA
Perennial Forb Density	NA	NA	NA	NA	-0.01 (-0.02, 0.01)	NA	NA	NA
Treatment Sites: Spring/Summer	NA	NA	NA	NA	NA	NA	NA	-0.17 (-1.85, 1.51)
Treatment Sites: Dormant	NA	NA	NA	NA	NA	NA	NA	<b>-1.73 (-3.30, -0.16)</b>
Spring/Summer Grazed × Post Treatment	NA	NA	NA	NA	NA	NA	NA	-0.17 (-1.96, 1.62)
Dormant Grazed × Post Treatment	NA	NA	NA	NA	NA	NA	NA	1.68 (-0.06, 3.41)

**Table 4**

Parameter estimates with 85% confidence intervals (LCL and UCL) from top AICc-selected logistic exposure models for sagebrush sparrow (Table 1) in southeast Oregon, USA, 2017–2019. See Table A1 for a list of all tested covariates, their descriptions, and summaries. Models listed in order of AICc ranking. Bold indicates 85% CI does not cross zero, NA indicates parameter is not present in model and <sup>2</sup> indicates a squared term. <sup>a</sup> 0.004, (−0.003, 0.01), <sup>b</sup> −0.02 (−0.034, −0.005), <sup>c</sup> −0.02 (−0.034, −0.003), <sup>d</sup> −0.02 (−0.033, −0.002), <sup>e</sup> 0.001, (0.0006, 0.0013), <sup>f</sup> 0.001 (0.0005, 0.0013).

Parameter estimates (85% CI)					
Parameter name	Model 1	Model 2	Model 3	Model 4	Model 5
Intercept	<b>6.50 (4.70, 8.29)</b>	<b>7.15 (4.96, 9.34)</b>	<b>6.18 (4.31, 8.05)</b>	<b>6.50 (4.70, 8.29)</b>	<b>5.70 (4.13, 7.28)</b>
Precip5day	<b>0.33 (0.01, 0.66)</b>	0.32 (−0.01, 0.66)	0.31 (−0.02, 0.65)	<b>0.33 (0.01, 0.65)</b>	<b>0.34 (0.03, 0.66)</b>
Precip5day <sup>2</sup>	<b>−0.02 (−0.03, −0.01)</b>	<b>−0.02 (−0.02, −0.01)</b>	<b>−0.02 (−0.02, −0.01)</b>	<b>−0.02 (−0.02, −0.01)</b>	<b>−0.02 (−0.02, −0.01)</b>
MaxT_5day	<b>−0.08 (−0.14, −0.02)</b>	<b>−0.08 (−0.14, −0.02)</b>	<b>−0.08 (−0.14, −0.02)</b>	<b>−0.08 (−0.15, −0.02)</b>	<b>−0.07 (−0.13, −0.01)</b>
Low Sage Density	<b>−4.55 (−7.33, −1.77)</b>	<b>−4.38 (−7.11, −1.64)</b>	<b>−4.77 (−7.60, −1.94)</b>	<b>−4.27 (−7.16, −1.37)</b>	<b>−4.01 (−6.80, −1.21)</b>
Camera Present	<b>0.93 (0.47, 1.38)</b>	<b>0.93 (0.47, 1.39)</b>	<b>1.06 (0.54, 1.58)</b>	<b>0.92 (0.47, 1.38)</b>	<b>0.64 (0.21, 1.06)</b>
Grazed Sites	<b>−0.82 (−1.38, −0.26)</b>	<b>−1.64 (−3.17, −0.12)</b>	<b>−0.87 (−1.44, −0.31)</b>	NA	<b>−0.75 (−1.30, −0.20)</b>
PrePost: Post Treatment	<b>−0.72 (−1.25, −0.19)</b>	<b>−1.57 (−3.12, −0.03)</b>	<b>−0.90 (−1.51, −0.28)</b>	<b>−0.72 (−1.25, −0.19)</b>	NA
Treatment Sites: Spring/Summer	NA	NA	NA	<b>−0.70 (−1.37, −0.02)</b>	NA
Treatment Sites: Dormant	NA	NA	NA	<b>−0.85 (−1.41, −0.29)</b>	NA
Breeding Season Precipitation	NA	NA	<sup>a</sup> 0.00 (0.00, 0.01)	NA	NA
Grazed Sites × Post Treatment	NA	0.99 (−0.62, 2.59)	NA	NA	NA
Precip 5-day × Avg Max Temp 5-day	<sup>b</sup> <b>−0.02 (−0.03, −0.00)</b>	<sup>c</sup> <b>−0.02 (−0.03, −0.00)</b>	<sup>d</sup> <b>−0.02 (−0.03, −0.00)</b>	<sup>b</sup> <b>−0.02 (−0.03, −0.00)</b>	<sup>b</sup> <b>−0.02 (−0.03, −0.00)</b>
Precip5day <sup>2</sup> × Avg Max Temp 5-day	<sup>e</sup> <b>0.00 (0.00, 0.00)</b>	<sup>e</sup> <b>0.00 (0.00, 0.00)</b>	<sup>f</sup> <b>0.00 (0.00, 0.00)</b>	<sup>e</sup> <b>0.00 (0.00, 0.00)</b>	<sup>e</sup> <b>0.00 (0.00, 0.00)</b>



**Fig. 4.** Predicted effect of A) the interaction of daily (time-varying) maximum temperature (°C) averaged across 5-days and daily (time-varying) precipitation (mm) accumulated across 5-days and B) density of low sagebrush per 1 square meter within a site on Daily Survival Rate (DSR) for sagebrush sparrow nests in southeast Oregon, USA 2017–2019. Predictions shown for the top AICc-selected model while holding all other predictor variables at their median values for continuous variables and post-treatment, grazed sites and camera for categorical variables, where applicable. Error bars and dashed lines represent 85% prediction intervals calculated using bootstrapping at 1000 iterations. Interactive graphs found at: (A) <https://rpubs.com/schroeva/848804>. See Table A1 for detailed variable descriptions.

Our estimates of DSR were lowest when nests experienced 5 days of very hot ( $>30^{\circ}\text{C}$ ) and very dry ( $<10\text{ mm}$ ) conditions (Fig. 4A). We also found that DSR was lower, under rainy and moderate temperature conditions, between average maximum temperatures of  $12\text{--}20^{\circ}\text{C}$  and  $>20\text{ mm}$  of cumulative precipitation in 5 days (Fig. 4A). Conversely, DSR was relatively high regardless of temperature in the intermediate levels of precipitation (between  $\sim 10\text{--}25\text{ mm}$ , Fig. 4A). Very hot and wet conditions and cold and dry conditions also resulted in higher DSR (Fig. 4A). Nests with cameras experienced higher DSR regardless of location (Table 4). All five competitive models included density of low sagebrush as a covariate, and higher density of low sagebrush was associated with lower DSR (Fig. 4B, Tables 2 and 4).

#### 4. Discussion

Effective conservation relies on understanding the respective roles and interactions of management and natural drivers of population dynamics. Livestock grazing, a primary land-use across much of the world and especially the western US, has not previously been connected to songbird nest success in the sagebrush ecosystem. We did not document a clear effect of grazing on daily nest survival for either species, suggesting the need for longer term studies. We hypothesized that the mechanisms driving a grazing effect on nest survival could be contributed to decreased herbaceous nesting cover, food resources or altered predator-prey dynamics. While we found that cattle grazing reduced site-level perennial bunchgrass cover post-treatment, no herbaceous cover variables were informative for explaining differences in daily survival rate among our nests, which indicates any effects from moderate grazing would most likely be from grazing induced changes to food resources, predator dynamics or potentially from vegetation measured at another spatial or temporal scale. Similar to other studies, we found that weather was an important factor explaining daily nest survival (Hightower et al., 2018; Macdonald et al., 2013; Rotenberry and Wiens, 1991). Both species suffered more nest failures when nests experienced higher levels of precipitation. While we found no support for grazing related vegetation differences explaining DSR, we did find limited evidence that vegetation not associated with grazing influenced DSR of both sparrow species.

Livestock grazing can influence the abundance and species composition of invertebrates (Borges and Brown, 2001; Goosey et al., 2019; Lee and Wall, 2006; Siemann, 1998; Skidmore, 1991; Wenninger and Inouye, 2008), which songbirds rely upon for adult and chick survival. Alternatively, grazing can influence predatory species diversity and abundance, a relationship that can vary by grazing intensity and species (Bich et al., 1995; Bylo et al., 2014; Jones and Longland, 1999; Jones et al., 2003; Larson, 2014). Daily nest survival in our study was lower during the post-treatment compared to the pre-treatment time frame for both species, and this effect was independent of grazing treatment. We also found site differences among grazed and non-grazed plots for both species. However, neither of these effects indicated a negative effect of grazing based on our BACI design for either species. For Brewer's sparrow, we found no evidence that grazing influenced DSR, and while the interactive treatment effect (grazed sites  $\times$  pre-/post-treatment) for sagebrush sparrows was competitive with the top model ( $\Delta\text{AIC}_c = 1.08$ ), the effect was not precise at 85% CIs. Two years was a relatively short timeframe to assess the effects of grazing regimes on sparrow nest survival, and the effects of grazing treatments may shift positively or negatively through time. Livestock grazing reduces herbaceous cover, directly affecting the plant community, a pattern supported by our results, where grazing at moderate levels reduced perennial bunchgrass cover in grazed sites relative to controls by roughly 30% and 15% on average in rotationally grazed and dormant grazed sites, respectively (Fig. 2). The lack of a negative grazing treatment effect (grazed sites  $\times$  time) for either Brewer's or sagebrush sparrows suggests reduced herbaceous cover due to grazing did not play a large role in the DSR of either sparrow species, which is a finding supported by other research in the sagebrush ecosystem (Fig. 2A, Tables 3–4, Chalfoun and Martin, 2007; Chalfoun and Martin, 2010). Our results regarding effects on plant communities were unsurprising in the context of recent literature, as long-term moderate cattle grazing only has modest effects on sagebrush plant community composition and structure (Davies et al., 2018). Furthermore, Borgmann and Conway (2015) found that 74% of avian studies assessing the effect of concealment on DSR have found no such effect, and most studies that find an effect of grass height had confounding bias as the result of measuring grass at failed nests earlier in the season than successful ones (Gibson et al., 2016; McConnell et al., 2017; Smith et al., 2018c). Research examining the effects of grazing on reproductive success metrics focused on potential mechanisms behind grazing effects, such as changes in invertebrate food resources or the nest predator community, are needed to better understand the role grazing plays in these complex ecosystems.

Precipitation and temperature can significantly affect reproductive success in passerines (Chase et al., 2005; Macdonald et al., 2013; Pérez et al., 2016). Both sparrow species in our study were influenced by within-year weather variation, and experienced declines beyond precipitation thresholds. While wetter years are generally associated with higher reproductive success (Gaston et al., 2005; Morrison and Bolger, 2002; Rotenberry and Wiens, 1991), within-year precipitation has been associated with declines in daily nest survival (Collister and Wilson, 2007; Macdonald et al., 2013), patterns supported by our data. We found daily nest survival for sagebrush sparrow declined when precipitation levels and temperatures were unseasonably hot ( $>30^{\circ}\text{C}$ ) and dry ( $<10\text{ mm}$  over 5 days) or temperate and wet conditions (Fig. 4A). Temperatures in excess of  $30^{\circ}\text{C}$  likely approach critical thresholds for this species, potentially resulting in reduced fitness (Cunningham et al., 2013). In addition to physiological stress on the adults and nests, extreme heat and low precipitation usually coincide with senescing vegetation and reduction in potential resources. More surprisingly, DSR declined, albeit not as drastically, under rainy and temperate conditions, when nests experienced maximum temperatures within the range of  $12\text{--}20^{\circ}\text{C}$  and over  $20\text{ mm}$  of cumulative precipitation in 5 days. We did not find this effect for Brewer's sparrows. This perhaps could be due to increased movement of the sagebrush sparrows on and off the nest under favorable conditions on a day-to-day basis, which may lead to increased opportunities for depredation events. Researchers have documented female songbirds spending less time off nest during periods of lower ambient temperatures (Amininasab et al., 2016; Conway and Martin, 2000). This could also be related to predation rates as Cox et al. (2013) documented higher nest predation rates by snakes and birds as maximum temperatures increased, plateauing above  $37^{\circ}\text{C}$ , and a peak in predation from mammals between around  $20\text{--}30^{\circ}\text{C}$ . Alternatively, wet conditions

may have been more physiologically stressful to clutches and/or broods when weather conditions were minimally conducive for adults to leave the nest. Overall, precipitation played a larger role in determining DSR than temperature, as DSR remained high in intermediate levels of precipitation (10–36 mm) regardless of temperature (Fig. 4). DSR remained high under hot and wet and cold and dry conditions (Fig. 4). This relates to field observations where excessive precipitation under cold or moderate temperatures may be physiologically stressful to clutches and broods, as nest material may remain wet long after the precipitation ceases under these conditions, whereas it may evaporate and dry under higher temperatures. In contrast, Brewer's sparrows appeared resilient to most weather conditions. While we detected an effect of precipitation, where DSR declined drastically with high amounts of cumulative precipitation over a 10-day period; however, these largest effects also had high variability in our DSR estimates (Fig. 3A). [Rotenberry and Wiens \(1991\)](#) conducted the most comprehensive study on weather and sagebrush-obligate songbird reproductive metrics and reported higher overall reproductive success for both Brewer's and sagebrush sparrows in wetter years but found that while sagebrush sparrows responded to within-year weather variation, Brewer's sparrows did not, results similar to our findings. The authors suggested Brewer's sparrows buffered this variation by altering clutch size, thus their reproductive investment ([Rotenberry and Wiens, 1991](#)). Brewer's sparrows tended to nest higher in shrubs, and the effect of nest height suggested nests higher in the shrub had higher DSR (Fig. 3B). Brewer's sparrows arrive at breeding grounds later than sagebrush sparrows, thus typically experience warmer temperatures on average. Brewer's sparrows were documented during this study fanning chicks on extremely hot days; however, sagebrush sparrows that nest closer to the ground than Brewer's sparrows were not observed fanning chicks. Thus, Brewer's sparrows may have evolved strategies to mitigate temperature stress on chicks whereas sagebrush sparrows have not.

During our study, extreme weather conditions had a larger influence on DSR than grazing management. Our results suggest that projected changes in climate and weather are a threat to the persistence of these species in many areas of the sagebrush ecosystem. The expectation of increased variability in summer temperatures and associated extreme temperature days ([Meehl et al., 2016, 2000](#)) and greater frequency and intensity of heavy precipitation due to climate change ([Easterling et al., 2017](#)) may have mixed effects on sagebrush-obligate songbird reproductive success. Over the next century, temperatures are projected to rise between roughly 2 and 6 °C in the Pacific Northwest with the summer months experiencing the greatest changes ([Almazroui et al., 2021; IPCC, 2007](#)). Climate precipitation models generally indicate larger inter- and intra-annual variation with drier summers, and wetter winters consisting of more rain and associated decreased snow cover and depth ([Almazroui et al., 2021; IPCC, 2007](#)). A shift to larger, less frequent precipitation events ([IPCC, 2007; Polley et al., 2013](#)) may be problematic for sagebrush sparrows as both precipitation extremes appear to drive DSR regardless of temperature. However, fledging success represents only one portion of reproductive success, and these species may be able to retain population viability through other demographic rates or behavioral changes in other life history stages, which may mediate the effects of a changing climate. The apparent resilience of Brewer's sparrows suggests adaptability to changes in weather relevant to future climate projections. Climate projections forecast bad news for sagebrush sparrows not only in terms of their nest survival, but in climate driven processes contributing to landscape scale loss of the sagebrush ecosystem, such as an unprecedented rise in frequency and intensity of wildfire, woody encroachment and invasion by exotic species ([Coates et al., 2016b; Miller et al., 2014; Mohamed et al., 2011; Pechony and Shindell, 2010; Polley et al., 2013](#)). Our results indicated that variable weather presents a much greater threat to these birds than reductions in herbaceous cover caused by moderate grazing under the studied conditions. While managers cannot control the weather, they can work to promote habitat conditions that foster population resilience to extreme weather. Weather conditions vary temporally and spatially; therefore, larger tracts of contiguous habitat increase the likelihood that favorable weather conditions would occur in potential nest locations across the landscape within a given year. Thus, landscape-scale management that maintains or increases quality habitat and decreases fragmentation would likely reduce the susceptibility of songbirds to extreme weather at the population level ([Newson et al., 2014](#)). Ultimately, management should focus on conserving extensive tracts of suitable habitat to increase songbird populations and their resiliency to increasingly variable and extreme weather conditions.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02010](https://doi.org/10.1016/j.gecco.2022.e02010).

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