Fire disturbance influences endangered Cape Sable Seaside Sparrow (*Ammospiza maritima mirabilis*) relative bird count

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Abstract

Periodicity of fire disturbance is a known driver of ecosystem function and is reported as important in both promoting and maintaining viable breeding habitat for the endangered Cape Sable Seaside Sparrow (*Ammospiza maritima mirabilis*, CSSS). In south Florida, the CSSS serves as a fine-scale indicator of the marl and mixed-marl prairie communities of the Florida Everglades. The CSSS distribution is affected by numerous well-documented physical drivers, including water depth and fire regime. Here, we fit zero-inflated negative binomial generalized linear mixed models and used model selection to determine the relationship between CSSS bird count observations from 1992 to 2014 and the spatially-specific fire return interval on the landscape. CSSS bird count was highest at a 5–8-year fire return interval and increased linearly with the percent of cell burned (400 × 400 m cells). The results of this study can inform management plans designed to maintain existing, and promote new, marl prairie habitat for conservation of the CSSS.

Keywords

avian, bird count, burn frequency, Everglades National Park, Everglades restoration, fire interval, marl prairie

1 | INTRODUCTION

Mixed marl prairie habitat is one of the most diverse floral and faunal communities in Florida's Everglades, a vast subtropical wetland that provides seasonally varying resources that support food webs across multi-annual cycles. Restoration success requires an understanding of the factors affecting ecosystem and wildlife population health (Hobbs & Harris, 2001; Ruiz-Jaen & Aide, 2005), including the effect of disturbance. In the Everglades, the Cape Sable Seaside Sparrow (CSSS: *Ammospiza maritima mirabilis*) is strongly associated with, and a key indicator of, marl and mixed marl prairie communities (Elderd & Nott, 2008; Lockwood et al., 2001). The CSSS is federally endangered (U.S. Fish and Wildlife Service, 1999), non-migratory, endemic to south Florida, and restricted to freshwater prairies of Everglades National Park (ENP) and Big Cypress National Preserve (BICY). The formation and maintenance of suitable CSSS habitat is viewed as a critical means to the recovery and persistence of CSSS subpopulations (Sustainable Ecosystems Institute, 2007), and is an important goal and measure of Everglades restoration success (Davis, Gaiser, Loftus, & Huffman, 2005; Pearlstine et al., 2016).

Changes in Everglades hydrology have resulted in reductions to CSSS habitat (Nott et al., 1998), and a concomitant 50% CSSS population decline from 1981 to 2015 (U.S. Fish
and Wildlife Service, 2016). Marl prairie community is located in short-hydroperiod areas inundated for 4–6 months out of the year, often dominated by muhly grass (*Muhlenbergia filipes*; Elderd & Nott, 2008), and supported by intermediate disturbance, such as fire, drying, and flooding (Kushlan et al., 1982). The CSSS nests at a preferred mean vegetation height of 14–18 cm (Lockwood et al., 1997; Werner, 1975), and nests are often lost to predators (e.g., small mammals; Baiser, Boulton, & Lockwood, 2008) when water levels rise above approximately 15 cm (Lockwood et al., 1997; Lockwood et al., 2001), making the timing of high water levels important, especially for egg survival and fledging success (Lockwood et al., 1997; Werner, 1975). However, the direct role of fire in maintaining suitable CSSS habitat is less clear.

Fire may support desirable habitat for the CSSS (Post & Greenlaw, 1994), preventing woody encroachment and excess litter accumulation. Anecdotal reports at the local site-scale have CSSSs returning to marl prairie habitat 3 years after a site has burned, but vegetation cover and composition can take much longer to recover, especially if there is rapid reflooding post-burn (Sah et al., 2009). Werner and Woolfenden (1983) reported that CSSS population density was highest with a 3-year fire interval in a densely vegetated *Muhlenbergia* prairie area in eastern Everglades National Park, and that the population density of CSSSs decreased with a decrease in the ratio of living to dead plant matter. Previous reports recommend burning approximately every 5 years on dense muhly grass prairie sites and approximately every 8–10 years at less densely vegetated muhly grass prairie sites (Kushlan et al., 1982). Additionally, there are conflicting reports that CSSS may not be dependent on fire. For example, CSSS densities and nest success in the southern portion of subpopulation E were not enhanced by fires, where CSSS density declined for 2 years after a fire, but then returned to levels similar to adjacent unburned areas 3 years after a fire (La Puma, Lockwood, & Davis, 2007). Further investigation at the landscape-level is needed to better understand the role of fire disturbance in maintaining CSSS populations.

We used CSSS bird count observations from 1992 to 2014 to investigate whether CSSS bird counts are influenced by landscape-scale fire return interval and the percent of area burned (in 400 × 400 m cells), to better understand how to increase suitable habitat for the CSSS; we predict high bird counts at a 5–6 year fire return interval and greater percent of cell burned.

## METHODS

### 2.1 Study area and Cape Sable Seaside Sparrow observations

The study area comprised all potential CSSS habitat within ENP (bounding box: 25°45′35″N–25°16′30″N, 81°10′28″W–80°30′35″W; Figure 1). The CSSS surveys were conducted by ENP via helicopter to sites on a 1-km grid (Kushlan & Bass Jr., 1983; Pimm et al., 2002; Virzi, Davis, & Slater, 2017) that encompassed all critical habitat areas (i.e., subpopulations). Observers waited 3–5 minutes after set-down and recorded all CSSS calls detected over a 7-min interval within an approximately 200-m radius of the set-down location; surveys are completed before 09:00 a.m. and discontinued in high wind or inclement weather. For further details on survey methods, see...
Pimm et al. (2002) and Virzi et al. (2017). We used CSSS observations (March-June, 1992–2014; \( n = 12,378 \)) as the estimate of the spatial distribution of CSSS relative bird count in ENP.

### 2.2 Historical fire data

Historical fire data were obtained over the ENP spatial extent from the EVER Fire Geodatabase (Smith, Foster, & Jones, 2015), which contains spatial delineations of fires digitized with aerial photography of fire scars and coordinate information from fire reports from 1983 to 2014. For a subset of the EVER Fire Geodatabase (1994–2004), fire perimeters were also visually compared to Landsat satellite imagery (Smith et al., 2015). For each year, we spatially summarized the fire history within Everglades Depth Estimation Network (EDEN) \( 400 \times 400 \) m grid cells (Jones & Price, 2007; Palsenau & Pearlstine, 2008). For each cell, we calculated the years since fire and the percent of the \( 400 \times 400 \) m cell burned using Spatial Analyst in ArcGIS 10.3.1 (Environmental Systems Research Institute, 2015); we set the maximum number of years since fire to 10 because marl prairie vegetation reaches recovery after 8 years post-burn (Sah et al., 2007). We removed CSSS observations when a fire was recorded the same year (\( n = 402 \)), because we were unable to determine if the fire occurred before or after the observation (observations for analyses: \( n = 11,976 \)).

### 2.3 Relationship between bird count and years since fire

We conducted all analyses in R version 3.4.4 (R Core Team, 2018). To determine the relationship between CSSS relative bird count and years since fire, we fit a fully interactive generalized linear mixed model with the glmmTMB package (Brooks et al., 2017) with the relative bird count as the response variable. Prior to running the model, we determined the data followed a negative binomial error distribution and were zero-inflated using the pscl package (Jackman, 2017) in R, by testing for the distribution using model goodness-of fit with a \( \chi^2 \) test based on the residual deviance and degrees of freedom, and for zero-inflation by testing for overdispersion in the count part of the zero-inflated model. We also applied model comparison methods with Corrected Akaike information criterion (AICc) and model weights (\( \omega \); see Table 1) using the MuMln package (Barton, 2018) in R to verify that the most parsimonious model was the zero-inflated negative binomial model.

Next, we applied the model selection to determine the most parsimonious model containing predictors of CSSS bird count using AICc and \( \omega \) (MuMln package; Barton, 2018). The fully interactive model contained a fixed effect of years since fire (1–10; both linear and quadratic terms), fixed effect of the percent of cell burned (0–100%), an interaction between years since fire and the percent of cell burned, and subpopulation as a random effect (subpopulations A–F). The fully interactive model did not converge because of a non-positive-definitive Hessian matrix (e.g., quasi-or-complete separation from high standard error and low sample size); after we removed the interaction between years since fire and the percent of cell burned, the model converged. After we selected the top model, we compared the top model to the null model using a \( \chi^2 \) test-statistic. We also predicted the mean expected bird counts (for the entire study area and study period [March–June, 1992–2014]) based on the relationships between each of the model parameters and the response variable in the top model, while holding the other model parameters at their mean, and estimated 95% confidence intervals around the model predictions of expected bird counts.

This research used previously collected data, and therefore did not require ethics approval.

### 3 RESULTS

The top model describing CSSS relative bird counts, determined using AICc and \( \omega \) (Table 2), contained a quadratic

| Model | Parameters (df) | AICc | \( \Delta \)AICc | \( \omega \) (weight) |
|-------|----------------|------|---------------|-------------------|
| Zero-inflated negative binomial 1* | 7 | 14,793.95 | 0.00 | 0.99 |
| Zero-inflated Poisson | 7 | 14,804.43 | 10.48 | 0.01 |
| Negative binomial 1 | 6 | 14,987.63 | 193.68 | 8.73E-43 |
| Zero-inflated negative binomial 2b | 7 | 15,036.92 | 242.97 | 1.72E-53 |
| Poisson | 6 | 15,057.67 | 263.72 | 5.39E-58 |
| Negative binomial 2 | 6 | 15,217.70 | 423.75 | 9.58E-93 |

Abbreviations: df, degrees of freedom; AICc, corrected Akaike information criterion; \( \Delta \)AICc, increase in AIC from the model with the best error structure.

*Negative binomial 1 = variance increases linearly with the mean.

bNegative binomial 2 = variance increases quadratically with the mean.
fixed effect of years since fire ($\beta = -0.016, p < .001$), a linear fixed effect of years since fire ($\beta = 0.222, p < .001$), a linear fixed effect of the percent of cell burned ($\beta = 0.002, p < .001$), and accounted for the random effect of subpopulation (subpopulation A: $\beta = -0.798$, B: $\beta = 1.71$, C: $\beta = -0.166$, D: $\beta = -0.736$, E: $\beta = 1.252$, F: $\beta = -1.224$; all parameter estimates are on the $\ln$ scale). The top model was significantly better than the null model, as explained by a $\chi^2$ test-statistic comparing the top model to the null model ($\chi^2 = 2020.4, p < .001$). The CSSS expected relative bird count peaked between 5 and 8 years after fire (Figure 2) and increased linearly with the percent of cell burned (Figure 2).

### TABLE 2

Model selection was conducted by comparing Corrected Akaike information criterion and model weights

| Model                                      | Parameters (df) | $\text{AICc}$ | $\Delta\text{AICc}$ | $\omega$ (weight) |
|--------------------------------------------|-----------------|----------------|----------------------|-------------------|
| Years since fire (quad), Percent burned    | 7               | 14,793.95      | 0.00                 | 0.88              |
| Years since fire (quad)                    | 6               | 14,797.96      | 4.01                 | 0.12              |
| Years since fire (linear), Percent burned  | 6               | 14,807.82      | 13.87                | 8.58E-04          |
| Percent burned                             | 5               | 14,817.30      | 23.35                | 7.47E-06          |
| Years since fire (linear)                  | 5               | 14,834.21      | 40.26                | 1.59E-09          |
| Null                                       | 3               | 16,806.32      | 2012.37              | 0                 |

**Note:** The top model explaining Cape Sable Seaside Sparrow (*Ammospiza maritima mirabilis*) bird count contained a quadratic (quad) fixed effect of years since fire, linear fixed effect of years since fire, linear fixed effect of the percent of cell burned; all models contained a random effect of subpopulation.

**FIGURE 2** (a) Model prediction of the expected Cape Sable Seaside Sparrow (*Ammospiza maritima mirabilis*) mean bird count peaks between 5 and 8 years since fire for the top model, and (b) there is a positive relationship between the percent of cell burned (400 x 400 m grid cells) and Cape Sable Seaside Sparrow expected mean bird count (predicted values are low because the data contain 47.5% zeros). Model predictions of expected mean bird counts were determined for the entire study area and study period (March–June, 1992–2014).

### 4 | DISCUSSION

The CSSS subpopulations are a landscape-scale indicator of the marl and mixed-marl prairie community in the Florida Everglades (DeAngelis et al., 2003; Pearlstine et al., 2016). The CSSS is particularly vulnerable to disturbance regime alterations (U.S. Fish and Wildlife Service, 1999), because of their restricted range and factors such as Allee effects in small subpopulations (subpopulations C, D, and F each contain <100 individuals; Elderd & Nott, 2008; Pearlstine et al., 2016; U.S. Fish and Wildlife Service, 1999). The low counts in subpopulations C, D, and F are difficult to model independently (Sah et al., 2009). In line with our predictions, the CSSS expected relative bird count across the landscape peaked between 5 and 8 years after fire, and increased linearly with the percent of cell burned (0–100% on 400 x 400 m grid cells; relative bird count was greater when a greater percent of the cell was burned), while accounting for critical habitat area subpopulations (A–F). More specifically, the finding of a predicted bird count of 0.12 birds at 1–2 years since fire compared to 0.19 birds at
5–8 years since fire represents a 56.4% increase in the mean expected bird count. Although the 95% confidence intervals are broad, we attribute this to the high level of zero-inflation (data contain 47.5% zeros) in the data set, because the CSSS is both rare and difficult to detect (e.g., see Virzi et al., 2017). Despite this, our model is significant, owing to a high magnitude of difference in mean bird count across years since fire and small standard errors (standard errors of the mean bird count range from 0.01–0.06 across 1–10 years since fire).

The role of disturbance, and specifically fire, is a significant force affecting ecosystem function (Hobbs & Cramer, 2008) and a factor in maintaining suitable habitat (e.g., for breeding) for CSSSs (Post & Greenlaw, 1994). Intermittent fires constrain encroachment of hardwood and dense grass, and the accrual of dead plant material, which are undesirable for CSSS nesting (Pimm & Bass Jr., 2002). In the Everglades, many plant and animal communities tolerate or require periodic burning (Beckage, Platt, Slocum, & Panko, 2003; Robertson, 1953). In our landscape-scale study, the CSSS relative bird count was highest at a fire interval of 5–8 years, which is supported by limited studies conducted on a small-scale (Kushlan et al., 1982; Sah et al., 2009; Werner & Woolfenden, 1983). Our results also support the evidence that too frequent fires are detrimental to CSSS suitable habitat (Curnutt et al., 1998), because vegetation cannot grow to CSSS nesting height (14–18 cm; Lockwood et al., 1997; Werner, 1975).

There are seven identified extant subspecies of the seaside sparrow (Ammospiza maritima; Post & Greenlaw, 2018), and our work is in agreement with the general conclusion that fire frequencies that are either too frequent (e.g., every year; Gabrey & Afton, 2004; Mitchell, Gabrey, Marra, & Erwin, 2006) or too infrequent (Kern, Shriver, Bowman, Mitchell, & Bounds, 2012; Mitchell et al., 2006) are not suitable for seaside sparrows in coastal marsh habitats, and periodic but infrequent fires are suggested as desirable to maintain seaside sparrow habitat (e.g., Gabrey, Afton, & Wilson, 2001). However, the optimal fire frequency for other subspecies of the seaside sparrow is reported as generally shorter compared to the CSSS, for example sparrow numbers were reported higher at 2 years post-burn in burned vs unburned marshes in Louisiana (A. m. fisheri; Gabrey et al., 2001; Gabrey & Afton, 2004), and a burn frequency of 1–4 years was suggested as desirable for seaside sparrow numbers in Maryland (A. m. maritimus; Kern et al., 2012), but it is also recognized that there is a lack of experimental studies that investigate the relationship between fire and seaside sparrows (Conway, Nadeau, & Piest, 2010; Gabrey & Afton, 2000; Mitchell et al., 2006).

Understanding the role of fire regime for the CSSS is relevant for maintaining a long-term fire management plan for Everglades marl prairie habitats. Recovery of the endangered CSSS has focused on appropriate water depths; here, we incorporated the landscape-scale effect of fire regime to better define management actions that can increase the area of seasonal breeding habitat. Natural fire regimes are altered due to fire suppression, but current protocol at ENP is to use prescribed fire and allow naturally ignited fires to burn unless they imperil cultural or natural resources (Lockwood, Ross, & Sah, 2003). The timing of a fire is also important because CSSS breeding peaks during the time of driest conditions in the Everglades (March–May), which can make CSSSs vulnerable to direct effects of fire during breeding. Fires that do not overlap with breeding are recommended for CSSSs (e.g., August–November; Kushlan et al., 1982; Werner & Woolfenden, 1983). Similarly, it may be important to control some of the natural and arson fires, because these often occur during the breeding season in April–May (Gunderson & Snyder, 1994).

Further analyses will examine CSSS responses to fire among a broader suite of environmental variables (e.g., hydrology, vegetation, spatial clustering) responsible for supporting marl prairie habitat and maintaining viable CSSS subpopulations across the landscape. Land managers are charged with making decisions regarding prescribed fires and the control of ignited fires in Everglades habitats. The results presented here on the fire component serve as an important tool for decision support in restoration and land management activities in the Florida Everglades marl prairie ecosystem.

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CONFLICT OF INTEREST

The authors declare there are no conflicts of interest associated with this publication. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

AUTHORS CONTRIBUTIONS

All authors meet the author contribution criteria, A.M.B. led the analyses and writing; J.M.B. advised on analyses and writing; L.G.P. provided the data, and advised on analyses.
and writing; S.S.R. advised on analyses and writing. All authors contributed to revision and preparation of the final version.

DATA AVAILABILITY STATEMENT

Data accessibility for these data is not permitted because it gives geographic coordinates of a federally listed endangered species.

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