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REVIEW

Endangered Cape Sable seaside sparrow ecology: actions towards recovery through landscape-scale ecosystem restoration

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ABSTRACT: Understanding the ecology of endangered taxa and the factors affecting their population growth and decline is imperative for their recovery. In the southeastern USA, the Everglades wetland ecosystem supports a high diversity of species and communities, including many endemic and imperiled taxa, such as the federally endangered Cape Sable seaside sparrow *Ammospiza maritima mirabilis* (CSSS). The Everglades, once a completely connected wetland with a slow-moving sheet flow of water, is now compartmentalized into separated wetland units where water distribution is managed year-round. The CSSS is affected by, and at the crux of, many Everglades ecosystem restoration decisions. The CSSS faces conservation challenges, including limited habitat availability, low population numbers, dispersal limitations, and constraints on suitable breeding conditions owing to wetland water levels. Despite these challenges, ecological knowledge of the factors affecting CSSS population numbers in the context of ongoing ecosystem-level restoration can help inform protection of this bird while restoring the Everglades. Existing research shows target hydroperiods between 90 and 210 days, a minimum of 90 consecutive dry days during the breeding season, and non-breeding season fires approximately every 5–10 years may aid in CSSS recovery. There are numerous tools and models to support habitat and water management for the CSSS, and the most recent ecosystem-level water operations plan for the Everglades indicates potential for increased CSSS habitat. Here, we provide a review on the ecology of the CSSS, factors affecting population decline, and ecosystem-level restoration actions that may aid in CSSS recovery.

KEY WORDS: *Ammospiza maritima mirabilis* · Everglades · Restoration · Marl prairie · Avian · Wetland · Hydrology · Fire · Imperiled

1. INTRODUCTION

Understanding the conditions that underlie the status of endangered taxa can help inform investment for population recovery (Male & Bean 2005). In the early 1990s, the US Fish and Wildlife Service (USFWS) adopted an ecosystem-based approach to wildlife conservation with the aim of perpetuating healthy ecosystems and limiting the necessity of future listings under the Endangered Species Act (ESA) (Beattie 1996). However, in some cases, species that are near extinction or occur only at small spatial scales may require more targeted and immediate conservation action to prevent extinction (Schwartz 1999).

In this review, we present information from disparate studies over the last 4 decades on the federally endangered Cape Sable seaside sparrow *Ammospiza maritima mirabilis* (CSSS) and identify how the science can help inform targeted conservation action

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through ongoing ecosystem restoration. The CSSS occupies the short-hydroperiod wetland marl prairie of the Florida Everglades, a habitat that has been reduced in both size and connectivity by alterations to the Everglades watershed, including agricultural conversion, urban expansion, and high water depths that do not support marl prairie vegetation in some parts of its range (Davis et al. 2005, Pearlstine et al. 2016). Conservation of the marl prairie has been a focus of ongoing ecosystem-based restoration in the Everglades, not only for the CSSS but also for the high plant species richness found in the marl prairie (Davis et al. 2005, Ross et al. 2006, Elderd & Nott 2008, Sah et al. 2011, 2015a), and the provision of habitat for many fishes, wading birds, and the iconic American alligator *Alligator mississippiensis* (Davis et al. 2005).

The Everglades is an expansive freshwater wetland system in the southeastern USA that is spatially and temporally dynamic, and although compartmentalized and managed, supports a diversity of species, including many endemic and imperiled taxa (USFWS 1999, Stein et al. 2000, Knight et al. 2011). The Everglades watershed was once a completely connected sheet flow of freshwater that spanned approximately 47 000 km^2 in Florida (Gleason & Stone 1994) and varied in depth seasonally as well as with topography and other factors. Because of water diversion and impoundment that began in the 1880s, the Everglades system has declined in area by 50% (Kushlan 1990, Kitchens et al. 2002, LoSchiavo et al. 2013) along with changes to the distribution of water across the landscape. In response to the modified hydrologic conditions in the Everglades, the US Congress passed the Comprehensive Everglades Restoration Plan (CERP) in 2000 (under the Water Resources Development Act of 2000, Public Law No. 106–541), to build infrastructure for hydrologic restoration and balance the needs of humans, wildlife, and the environment (RECOVER 2011, LoSchiavo et al. 2013). Water is continuously managed and moved between wetland compartments through almost 1400 water control structures such as pumps, gates, and levees, and over 4000 km of canals and levees (South Florida Water Management District 2010). Alterations to water depths, hydroperiods, water quality, and habitats (Ogden et al. 2005, LoSchiavo et al. 2013) have affected many imperiled taxa, including the CSSS (Nott et al. 1998, Curnutt et al. 2000, Pimm et al. 2002).

The federally endangered CSSS was included in the first issued list of endangered species (ESA 1973, as amended), and is at the forefront of conservation and restoration in the Everglades (Curnutt et al. 1998). Although the taxonomy and subspecific status has changed throughout the years (Davis et al. 2021), the CSSS has always been considered either its own species or subspecies, distinct from other seaside sparrows (Howell 1919, Howell 1932, Stimson 1968, Eisenmann et al. 1973, USFWS 1983, 1999, Klicka et al. 2014, Davis et al. 2021); therefore, management and recovery activities are assigned specifically to the CSSS (USFWS 1983, 1999, Slater et al. 2009). The most recent genetic studies classify the CSSS as *Ammospiza maritima mirabilis* (Klicka et al. 2014, Davis et al. 2021), in agreement with the North American Classification Committee of the American Ornithological Society (Chesser et al. 2018).

The CSSS is endemic to south Florida and is presently limited to 2 separate areas of marl prairie in the southern Everglades, in 6 identified subpopulations (Fig. 1; Walters et al. 2000, Davis et al. 2005, Virzi et al. 2009, USFWS 2020, Benscoter et al. 2021). The CSSS was first documented on Cape Sable in 1919 (Howell 1919), but is not currently found there. It was also historically observed in additional areas and habitats in south Florida where it is not currently found (e.g. salt marsh habitats; Nicholson 1928, 1934, Howell 1932, Anderson 1942, Stimson 1956, USFWS 1983, Werner & Woolfenden 1983). The CSSS is presently found in Everglades National Park, areas of Big Cypress National Preserve, and the state-owned Southern Glades Wildlife and Environmental Area. The population size of the CSSS has declined by over half since the early 1980s (USFWS 2020, Benscoter et al. 2021), along with declines in habitat extent.

The primary habitat of the CSSS, the marl prairie, is both limited and affected by the diversion and compartmentalization of the Everglades watershed and the ongoing restoration and management activities in the region. Both the hydroperiod and the fire regime affect the marl prairie species assemblage (Sah et al. 2011, 2015b) and presence of CSSS in an area (Ross et al. 2006), where hydroperiod represents the number of days in a year that a location is inundated with water. The marl prairie is seasonally flooded (Nott et al. 1998, Davis et al. 2005, Ross et al. 2006, Hanan et al. 2010), and fire reduces woody species (Werner & Woolfenden 1983) that are unsuitable for CSSS nesting (Pimm et al. 2002). Some areas where the CSSS has been documented have become too wet (e.g. longer hydroperiod than marl prairie habitat) and have converted to marsh vegetation types unsuitable for CSSS nesting, whereas other areas have become drier than marl prairie habitat (e.g. shorter hydroperiod), leading to increased fire

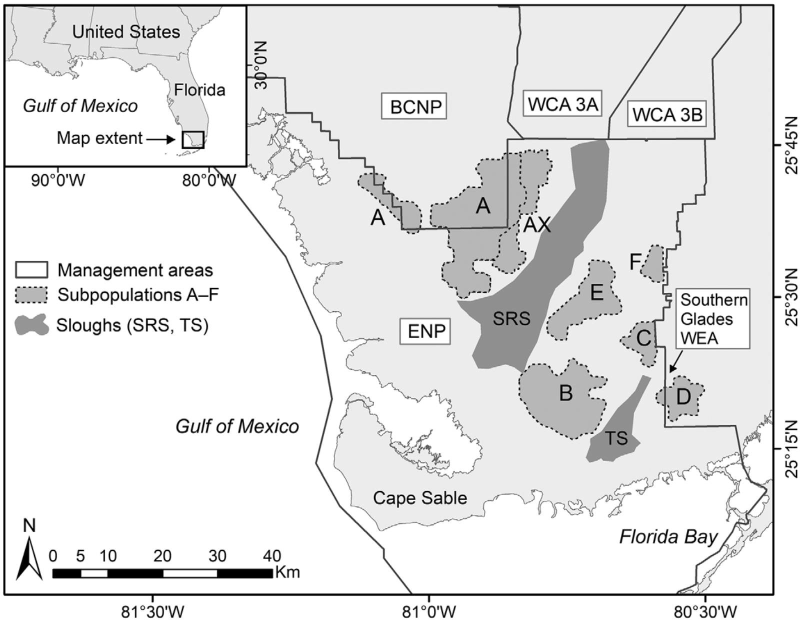

Fig. 1. Geographic range of the Cape Sable seaside sparrow (CSSS), comprising 6 subpopulations (A–F, where AX denotes expanded areas of subpopulation A on the eastern side identified as a potential future suitable area for the CSSS; USFWS 2020) located primarily in Everglades National Park (ENP), and also in portions of Big Cypress National Preserve (BCNP) and the Southern Glades Wildlife and Environmental Area (WEA). Water Conservation Areas (WCA) 3A and 3B are located to the north of CSSS subpopulations. Shark River Slough (SRS) and Taylor Slough (TS) represent deeper water areas that are not suitable for the CSSS

frequencies or woody encroachment (Pimm et al. 2002, Elderd & Nott 2008).

Because the CSSS exhibits limited movement and dispersal both within and between spatially isolated subpopulations (Lockwood et al. 2001), the separation of small subpopulations by unsuitable areas presents conservation challenges for recovery. Shark River Slough forms unsuitable, deeper water areas located in between the range of subpopulation A and all the other subpopulations (Fig. 1; Nott et al. 1998), and the CSSS subpopulations are surrounded by unsuitable areas such as water control structures (e.g. levees), roads, urban areas, agricultural areas, deeper water, or forested areas. Even in cases of longer-distance movements, individuals ceased traveling when they reached unsuitable areas (Dean & Morrison 2001). Restricted movement, dispersal, and isolated populations are common among seaside sparrows, pointing to the need to find management solutions in remaining habitat (Rising 2005).

This review contributes to an overall understanding of imperiled seaside sparrows, which are impacted by anthropogenic activities such as land cover conversion from urban expansion, sea level rise, and unsuitable fire regimes. Although seaside sparrows in general are considered of Least Concern by the International Union for Conservation of Nature Red List of Threatened Species (BirdLife International 2021), the CSSS is 1 of 9 recognized subspecies of the seaside sparrow, 7 of which are extant (2 extinct), that range along the Atlantic Ocean and Gulf of Mexico coasts of the USA (Nelson et al. 2000, Rising 2005, Davis et al. 2021). MacGillivray's seaside sparrow *A. m. macgillivraii* along the southern Atlantic coast of the USA has experienced similar challenges to its habitat as the CSSS, including habitat conversion for urban expansion, as well as inundation from sea level rise (USFWS 2018). In Florida, the dusky seaside sparrow *Ammodramus maritimus nigrescens* was declared extinct in 1990 (note that *Ammodramus maritimus* is now classified as *Ammospiza maritima*; USFWS 1990). Areas where the dusky seaside sparrow was once common in central and eastern Florida were converted to commercial and government uses in the 1960s and 1970s (Walters 1992). Remaining habitat was largely on ranch land and burned frequently during the dry season, which damaged dusky seaside sparrow habitat (Walters 1992). Similarly, another endangered Florida sparrow in the dry prairies of the central part of the state, the Florida grasshopper sparrow *Ammodramus savannarum floridanus*, requires fire to curb the encroachment of woody vegetation (Hewett Ragheb et al. 2019). A consortium of partners has taken focused conservation actions such as habitat management and captive breeding which have yielded some successes for this subspecies of sparrow (USFWS 2019). Similarly focused conservation actions for the CSSS by the relevant partners may be able to adequately recover the only existing CSSS population in the world.

Here, we provide a review of the ecology of the federally endangered CSSS, including factors associated with population declines, and a look at ecosystem-level restoration and management actions that have potential to aid in CSSS recovery. This review is important because the CSSS is at the core of many restoration and management issues in the Everglades (e.g. see Walters et al. 2000), and restoration and management practitioners are held accountable under the ESA for actions that negatively affect the

CSSS, including habitat modification and degradation (USFWS 2020). Additionally, there is an urgency for population recovery for the CSSS, because of overall population declines and the low numbers observed in some subpopulations, including what used to be the second largest subpopulation (subpopulation A; Curnutt et al. 1998, Nott et al. 1998, Cassey et al. 2007, USFWS 2020, Benscoter et al. 2021). Extinction risk is at play for the CSSS (Pimm & Bass 2002, Elderd & Nott 2008) and the USFWS population target of 6600 individuals (USFWS 1999, 2010) has not been met in any year from 1992 onwards (USFWS 2020, Benscoter et al. 2021). The population has not recovered even though scientists have studied the CSSS for over 4 decades.

2. POPULATION AND SUBPOPULATION TRENDS

The population size of the CSSS has decreased by approximately 63% since the original range-wide population survey was conducted in 1981 from approximately 6660 birds (USFWS 2020) to approximately 2450 birds in 2021 (Benscoter et al. 2021, T. Dean unpubl. data) (Table 1), with the CSSS remaining in 6 subpopulations (A–F; Fig. 1). The subpopulation estimates for 2021 were: A, 0 birds; B, 1488; C, 112; D, 288; E, 528; and F, 32 (Benscoter et al. 2021, T. Dean unpubl. data; estimates are subject to revision by Everglades National Park). Preliminary data from 2022 surveys estimate a slight increase to just over 2900 birds (T. Dean unpubl. data). Low subpopulation numbers are currently observed in subpopulations A, C, and F, and all 3 of these subpopulations have numbers that are much lower than in 1981. Notably, subpopulation A, which used to hold a high number of birds, declined in the early 1990s (Curnutt et al. 1998, Nott et al. 1998), and has not recovered (Curnutt et al. 1998, Nott et al. 1998, USFWS 2020). Although no birds were observed in the range-wide surveys for subpopulation A in 2021, 4 adult birds were observed in this subpopulation in both 2019 and 2020 during in-depth demographic monitoring (Virzi & Tafoya 2021), indicating that some birds may be currently present in subpopulation A. Subpopulation D has shown a recent increasing subpopulation trend, but numbers are still lower than they were in 1981 (Walters et al. 2000, USFWS 2020). Larger and relatively stable subpopulation numbers since 1981 have only been observed in 2 of the 6 subpopulations, B and E (Cassey et al. 2007, USFWS 2020, Benscoter et al. 2021).

Table 1. Cape Sable seaside sparrow subpopulation (A–F) and overall population (total) estimates beginning with the first year of the range-wide surveys (1981) and presented for approximately every 10 yr thereafter. Population estimates transcribed from USFWS (2020) and Benscoter et al. (2021); for more details on population estimation method see Kushlan & Bass (1983) and Walters et al. (2000)

Subpopulation	Year				
	1981	1992	2001	2011	2021
A	2688	2608	128	176	0
B	2352	3184	2128	1904[a]	1488
C	432	48	96	176	112
D	400	112	32	16	288
E	672	592	848	592	528
F	112	32	32	32	32
Total	6656	6576	3264	2896	2448

[a]Subpopulation B was not surveyed in 2011, so the 2010 estimate is provided

3. HABITAT

Habitat loss is the primary threat to biodiversity conservation globally (Brooks et al. 2002). As habitat extent is reduced, the remaining habitat can become too small to support viable populations of birds (Pimm & Askins 1995). Ongoing ecosystem restoration in the Everglades has the potential to increase habitat area and aid in the recovery of the CSSS.

3.1. Federally designated Critical Habitat

The federally designated Critical Habitat for the CSSS includes subpopulations B–F (Fig. 1; USFWS 2007), located in freshwater marl prairie habitat within Everglades National Park and the Southern Glades Wildlife and Environmental Area. The area of subpopulation A has been proposed for inclusion in Critical Habitat designation (USFWS 2006), but it was excluded in the most recent designation.

3.2. Freshwater marl prairie

The freshwater marl prairie community is the primary habitat of the CSSS, supports a diverse assemblage of graminoids and forbs, and is often dominated by grasses, sedges, and rushes (Walters et al. 2000, Davis et al. 2005), including *Muhlenbergia capillaris* var. *filipes* (hereafter '*Muhlenbergia*' or 'muhly grass'; Sah et al. 2021, Wunderlin et al. 2021; www.itis.gov) and *Schoenus nigricans* (hereafter '*Schoenus*'; Sah et al. 2021); *Muhlenbergia* dominates on the drier end of the hydrologic gradient within the marl prairie community (Davis et al. 2005, Ross et al. 2006, Elderd & Nott 2008). The marl prairie is located in a mosaic between deeper-water marsh (Sah et al. 2015a) and drier, higher-elevation areas containing trees (Werner & Woolfenden 1983), is seasonally flooded, and experiences periodic fire (Kushlan et al. 1982). Marl prairie communities can be flooded for 2–9 mo out of the year, but more commonly for 4–6 mo (Nott et al. 1998, Davis et al. 2005). Marl prairie vegetation types are aligned along a hydrologic gradient based on hydroperiod (Lockwood et al. 2003, Davis et al. 2005, Ross et al. 2006, Sah et al. 2015a).

Breeding habitat for the CSSS is constrained both spatially across the landscape and temporally during the year. The freshwater marl prairie is spatially limited to 2 areas located east and west of Shark River Slough (Nott et al. 1998), and bordered on all sides by unsuitable areas for CSSS breeding. The marl prairie extent is flanked on the northern side by water control structures and Tamiami Trail (US Highway 41) that create a hard division between Everglades National Park and Water Conservation Areas to the north, the eastern side by urban development and agriculture, and the western and southern sides by the saltwater of the Gulf of Mexico and Florida Bay (Nott et al. 1998). The marl prairie in southern Florida once extended farther north and east (Davis 1943), but spatial coverage and connectivity have decreased because of Everglades drainage and compartmentalization, agriculture, and urbanization (Kushlan et al. 1982, Davis et al. 2005, Elderd & Nott 2008). Other stressors on the marl prairie owing to water management include prolonged hydroperiods and flooding during the dry season in some areas (e.g. the western marl prairie), shortened hydroperiod and amplified drought in other areas (e.g. the northeastern marl prairie), including conditions leading to intense fires or non-native tree invasion in overly dry areas (Van Lent et al. 1999, Davis et al. 2005, Sah et al. 2015a). Temporally, breeding habitat for the CSSS is only available from approximately March through June depending on water levels (Lockwood et al. 1997, 2001, Pimm et al. 2002, Davis et al. 2005, Elderd & Nott 2008).

3.3. Hydrology and habitat: occupancy and abundance

High water levels and flooding have negative effects on CSSS occupancy and abundance (Bass & Kushlan 1982, Nott et al. 1998, Jenkins et al. 2003b, Cade & Dong 2008, Elderd & Nott 2008), and conversely, conditions that are too dry are linked to lower CSSS numbers (Ross et al. 2006), often attributed to increased fire frequency in dry areas (Pimm et al. 2002). The CSSS is more common in wet prairie areas with relatively short hydroperiods, dominated or co-dominated by *Muhlenbergia*, that are species rich, and where *Cladium* is not dominant (Pimm et al. 2002, Lockwood et al. 2003). Detailed vegetation surveys of numerous vegetation communities indicated that wet prairie (WP) community types had the greatest percent of survey sites where the CSSS occurred, including *Muhlenbergia* WP, *Schoenus* WP, *Schizachyrium* WP, and *Cladium* WP (Ross et al. 2006). Sites where the CSSS was observed the least were in marsh community types that had relatively longer hydroperiods (wetter) compared to WP, and were located mainly on the western and southeastern areas of the CSSS range. These wetter marsh communities that supported fewer sparrows included *Cladium*, *Rhynchospora*, and *Eleocharis* marshes (Ross et al. 2006).

3.4. Hydrology and habitat: reproduction

Peak breeding for the CSSS occurs from March through June, coincides with and is determined by the length of the dry conditions, and declines when water levels become too high (Lockwood et al. 1997, 2001, Pimm et al. 2002, Elderd & Nott 2008). Approximately 40 d of nearly dry conditions without fire are needed for successful CSSS nesting, and 60 d are needed for the initiation of a second clutch (Pimm et al. 2002), which is necessary for population growth (Walters et al. 2000). The CSSS builds cup or dome-shaped nests close to the ground (Pimm et al. 2002), away from shrubs and trees (Kushlan & Bass 1983, Pimm et al. 2002), woven into clumps of graminoid vegetation (Post & Greenlaw 1994) such as *Muhlenbergia* (Lockwood et al. 1997, 2001, Davis et al. 2005), at vegetation heights of 16–21 cm above the soil surface (Lockwood et al. 2001).

Water levels play a primary role in affecting breeding conditions for the CSSS, because it builds nests close to the ground. Conditions that are too dry prior to and at the onset of the breeding season can lead to delayed nest initiation and lower clutch size (Boulton et al. 2011), which may, thus, be related to food availability. High water and flooding during the breeding season can have negative effects on CSSS reproduction, including nest flooding (Nott et al. 1998, Lockwood et al. 2001), lowering nest survival (Boulton et al. 2011, Gilroy et al. 2012), and cessation of courtship and nesting activities (Lockwood et al. 1997, 2001) that may not resume even if water levels decrease to acceptable levels. The termination of CSSS breeding activities was documented when water levels rose to 18 cm (in late June), and even when water levels fell 4 cm (in mid-July), the CSSS did not resume breeding activity (Lockwood et al. 1997). The end of the CSSS breeding season coincides with the onset of the wet (rainy) season (June; Lockwood et al. 1997).

Nest survival for the CSSS is related to hydrologic conditions (Lockwood et al. 2001, Baiser et al. 2008, Boulton et al. 2011, Gilroy et al. 2012) and population growth for the CSSS is contingent upon high nest success rates, a second successful breeding attempt, and also high CSSS survival (Walters et al. 2000, Lockwood et al. 2001). Hydrologic variables such as seasonal water level and timing of nesting related to the occurrence of flooding predict nest success for the CSSS (Gilroy et al. 2012). In areas with water levels >29 cm, nearly 70% of active CSSS nests will fail because of nest flooding (Lockwood et al. 2001). Nests placed too low in the vegetation may be at risk of flooding, but nests placed too high may be unstable (e.g. graminoid vegetation is too thin to support the nest) or susceptible to adverse weather or predation (Walters et al. 2000). Additionally, increased nest and young predation risk is also associated with higher water levels (Lockwood et al. 1997, Pimm et al. 2002, Baiser et al. 2008). Similarly, nest success is lower for nests initiated later in the breeding season when flooding is more likely, compared to earlier in the breeding season (Walters et al. 2000, Lockwood et al. 2001, Boulton et al. 2011). Therefore, drying and flooding impacts from ecosystem-level hydrologic restoration and management activities in the Everglades can have substantial effects on the CSSS.

3.5. Fire and habitat

The effect of fire on the CSSS depends on factors such as timing, frequency, size, and interactions with other disturbances such as post-fire flooding. Despite the number of studies investigating fire related to the CSSS, the fire type or severity is often unknown (e.g. not recorded in the Everglades National Park fire database; Smith et al. 2015), and fire can interact with other environmental variables, making it difficult to form concrete conclusions.

The primary sources of fire in CSSS habitat include fire from lightning strikes, prescribed fire used for ecosystem management, and non-prescribed human-induced fires (accidental, e.g. escaped campfires, or intentional, e.g. arson) that are typically suppressed in Everglades National Park (Curnutt et al. 1998, Smith et al. 2015). Lightning-strike fires are typically documented from March to September, prescribed fires occur from November to March, and non-prescribed human-induced fires are reported from December to May (Curnutt et al. 1998). Dry-season fires (approximately December–May) usually burn more completely, whereas wet-season fires (approximately June–November) usually burn in a patchy pattern (Curnutt et al. 1998).

In general, periodic fire can help maintain marl prairie habitat for the CSSS, and can be a beneficial management tool; however, fires that occur too frequently, that cover a large portion of the area of a subpopulation, or occur during the breeding season may be detrimental. Intermittent fires benefit CSSS habitat via limitation of woody encroachment, overly dense grass, and excess litter accrual (Taylor 1983, Pimm et al. 2002). However, too frequent fires may negatively affect CSSS habitat (e.g. annual fires; Curnutt et al. 1998, Nott et al. 1998, Jenkins et al. 2003a) by limiting vegetation from growing to preferred CSSS nesting heights (e.g. 14–18 cm; Werner 1975, Lockwood et al. 1997). Marl prairie vegetation can recover within 2–4 yr after a fire (Taylor 1983, La Puma et al. 2007, Sah et al. 2011), but rapid flooding post-fire can limit vegetation recovery and lead to unsuitable vegetation communities for the CSSS (Sah et al. 2011, 2015b). Fires that occur during the breeding season can inhibit breeding (Werner & Woolfenden 1983) and lead to nest loss (Lockwood et al. 2003, Davis et al. 2005) and bird mortality (Werner 1975, Werner & Woolfenden 1983, Curnutt et al. 1998). Therefore, periodic managed fires during the non-breeding season are recommended for the CSSS (Kushlan et al. 1982, Werner & Woolfenden 1983).

Studies indicate a quadratic relationship between time since fire and both CSSS bird count and site occupancy patterns, with the greatest bird count between 5 and 8 yr since fire (data from 1992–2014; Benscoter et al. 2019) and the highest occupancy from 6 to 11 yr since fire (data from 1989–2005; La Puma 2010). A detailed study after the Lopez fire, a large human-ignited fire in the southern area of subpopulation E, showed that densities of the CSSS and nest success declined for 2 yr after the fire, but then returned to levels comparable to adjacent unburned areas 3 yr after the fire (La Puma et al. 2007). Because hydrologic conditions are linked to fire frequency (e.g. more frequent fires in drier areas; Ross et al. 2006), water management can modulate the degree to which fire impacts the CSSS and its habitat.

In conjunction with hydrologic management, fire management is a tool that can aid in CSSS recovery (NPS 2015). A revised Everglades National Park Fire Management Plan produced in 2015 provides a collaborative approach to fire management that considers the effects of fire management on species and habitats in Everglades National Park, including specific guidelines for the CSSS (NPS 2015). The Everglades National Park Fire Management Plan includes a science-based adaptive management framework to modify and improve fire management over time with options for both minimizing fires via suppression or allowing fires to burn. Additionally, the plan outlines ignition treatments adjacent to the locations of CSSS subpopulations to aid in fuel reduction to lower the probability of potential undesirable fires (e.g. high intensity fires) spreading into CSSS habitat as well as prescribed burning at the wildland–urban interface to avoid fires that burn over into neighborhoods and urban areas.

The Everglades National Park Fire Management Plan outlines fire return intervals for different habitats based on literature reviews and input from subject matter experts. The fire strategy for the CSSS is re-visited on an annual basis by the National Park Service (NPS), the USFWS, and other partners (NPS 2015). For the CSSS, the annual area treated with prescribed fire is set to <35% of CSSS Critical Habitat and <20% of occupied CSSS habitat, with no greater than half of the area of any subpopulation burned at one time (NPS 2015). The target fire return interval for managers to achieve is set to 3–12 yr for the marl prairie (i.e. muhly prairie). More specifically, the target fire return interval for marl prairie categorized as wildland–urban interface is 3 yr (the minimum), and 8 yr for marl prairie that is not wildland–urban interface, both with room for variability from 3 to 12 yr (NPS 2015). This fire management strategy for the CSSS aims to avoid the detrimental effects of large intense fires, while maintaining the beneficial effects of periodic fire for the CSSS and associated marl prairie habitat. The fire return interval of 3–12 yr set by the Everglades National Park Fire Management Plan (NPS 2015) is in line with research indicating that fires every 4–11 yr support the highest levels of CSSS occupancy and bird count (La Puma 2010, Benscoter et al. 2019) and that marl prairie vegetation can recover within 2–4 yr since fire, but may take longer if there is flooding post-fire (Sah et al. 2010, 2015b, La Puma et al. 2007).

3.6. Conservation implications: hydrology, habitat, and occupancy

Documented causes for declines in the number of sparrows in some subpopulations related to habitat conditions include alterations to water delivery into the marl prairie and changes in hydroperiod. Declines in CSSS numbers in subpopulation A are attributed to increased water deliveries and flooding in the early 1990s (Nott et al. 1998, Walters et al. 2000, Pimm et al. 2002, Cassey et al. 2007, Elderd & Nott 2008). Declines in CSSS numbers from wetter conditions are also documented for the lower area of subpopulation C, subpopulation D, and the southern and western areas of subpopulation E (Pimm et al. 2002). Declines in subpopulations F and areas of C are mainly attributed to a shift towards drier conditions than those which occurred historically, and atypically high fire frequencies beyond what is suitable for the CSSS (Nott et al. 1998, Walters et al. 2000). The area where subpopulation F is located has high densities of native and non-native shrubs (Curnutt et al. 1998), and woody encroachment is unsuitable for CSSS nesting (Pimm et al. 2002, Jenkins et al. 2003a). The hydrology of CSSS habitat is managed primarily because of the compartmentalization of the Everglades; thus it is possible to encourage CSSS population recovery through restoration and management actions in the Everglades ecosystem.

Hydrologic conditions influence the CSSS (Jenkins et al. 2003b, Cade & Dong 2008, Elderd & Nott 2008, Haider et al. 2021a,b) and its habitat (Nott et al. 1998, Jenkins et al. 2003a, Armentano et al. 2006, Ross et al. 2006); therefore, targeted hydrometrics that produce habitat for the CSSS are often investigated and implemented into ecosystem-level water management decisions. The USFWS set a target discontinuous hydroperiod of 90–210 d to promote the growth of marl prairie habitat (4 yr running average; USFWS 2010, 2020). Research on CSSS occupancy at sites located across all subpopulations indicated that CSSS presence was observed at approximately 50% of the sites with vegetation-inferred hydroperiods between 90 and 150 d, where vegetation-inferred hydroperiod was determined by evaluating the relationship between vegetation community groups and water inundation levels (Ross et al. 2006). Additionally, CSSS presence was observed at <20% of sites with inferred hydroperiods between 60–90 and 240–270 d, and the CSSS was rarely observed at sites with inferred hydroperiods >270 d (data from 2003–2005; Ross et al. 2006). A recent study modeling CSSS presence in relation to environmental variables found that CSSS presence between 1992 and 2005 was highest in areas with 4 yr mean hydroperiods between 80 and 120 d (EverSparrow model; Haider et al. 2021a), in agreement with Ross et al. (2006; 90–120 d most associated with CSSS presence), suggesting that the USFWS target (90–210 d) could potentially be refined to a narrower band (e.g. to drier conditions). Studies have also found the highest CSSS occupancy in dry conditions during the breeding season (water depths below ground level at ≤0 cm: Haider et al. 2021a; water depths between 0 and 25 cm: Beerens & Romañach 2016). However, the wider USFWS 90–210 d target is already challenging to meet (Beerens & Romañach 2016), and these studies indicate that the USFWS hydrologic target includes suitable hydroperiod ranges for the CSSS. In addition to achieving hydrologic conditions suitable for the CSSS, home range sizes and movement patterns can affect the ability of the CSSS to move to and use habitats as they become available.

4. TERRITORY, HOME RANGE, AND MOVEMENTS

Movement behavior, territory size, and home range extent can affect the ability of taxa to respond to environmental change when habitats become altered, reduced, fragmented, or isolated. Understanding space use and the potential for and limitations to movement and dispersal can help identify necessary conservation actions. The sedentary nature of the CSSS in addition to limited and fragmented habitat makes it critical to understand the environmental conditions of occupied habitat to better inform targeted restoration action.

4.1. Territory and home range

Understanding the territory and home range size of the endangered CSSS is important for recovery efforts because CSSS habitat is both limited and fragmented, and subject to change with restoration and water management. Males exhibit site fidelity to territories, both within and across breeding seasons (Werner 1975, Werner & Woolfenden 1983, Pimm et al. 2002). Territory establishment for the CSSS often begins in February (Pimm et al. 2002), and territories usually do not overlap among individuals, although a small amount of overlap may occur (Pimm et al. 2002, Cassey et al. 2007). Males defend their territories during the breeding season by singing (Werner & Woolfenden 1983, Pimm et al. 2002) and use territories for mating, nesting, feeding, and sheltering. The territory represents the core area of use (50% probability of locating the animal), and the home range represents the overall area of use (95% probability of locating the animal) during the breeding season (Virzi et al. 2016). Smaller and less variable male territory and home range sizes occur in CSSS subpopulations with higher bird counts (B, E; territory: mean ± SE = 1.7 ± 0.1 ha, home range: 7.2 ± 0.5 ha) compared to subpopulations with lower bird counts (A, C, D, F; territory: 10.3 ± 1.5 ha, home range: 42.1 ± 5.6 ha; Virzi et al. 2016; measured via GPS points for n = 373 males from 2006 to 2015). Additionally, paired males show smaller territory and home range sizes compared to unpaired males in the subpopulations with lower bird counts (Virzi et al. 2016). Other reported CSSS territory sizes include mean territory sizes of 1.4 ha (n = 52) in *Muhlenbergia* prairie in Everglades National Park and 3.6 ha (n = 10) in Big Cypress National Preserve (Werner & Woolfenden 1983; measured by recording locations of marked individuals) and a mean territory size of 2.36 ha (Pimm et al. 2002; measured from 1993 to 1996 by marking perch locations of singing males). During the non-breeding season, home ranges generally overlap more (Dean & Morrison 1998) and the CSSS generally use a greater area; however, the birds are still primarily sedentary and usually do not travel far from breeding territories (Dean & Morrison 2001).

4.2. Dispersal

The CSSS is philopatric (Lockwood et al. 1997, Dean & Morrison 1998, Pimm et al. 2002) and often does not disperse far from its natal area (Dean & Morrison 2001, Lockwood et al. 2001). The CSSS may move around after independence, but often switches to sedentary behavior at the onset of molt, and usually settles in an area within 6 mo of fledging (Dean & Morrison 2001). Resighted or recaptured juveniles from hatching locations indicate a mean natal dispersal distance of 577 m (SD = 980 m, n = 15), although juveniles are capable of dispersing distances greater than 1 km (Lockwood et al. 2001). Even though long-distance movements for juveniles are possible, individuals in a color banding and radio-transmitter study discontinued long-distance movements when they reached prairie habitat margins (non-breeding season study in subpopulation B from 1997 to 1999; Dean & Morrison 2001). Additionally, the upper 5 and 10% of the distribution of movement lengths between locations for juveniles were 519 and 345 m, respectively; 1 juvenile moved 4.92 km between locations (Dean & Morrison 2001). Eight inter-subpopulation movements were observed in the CSSS over a period of 10 yr in a capture, mark, and resight study, 3 of which were made by juveniles and the remaining by adults (from 3 subpopulations from 1997 to 2007; Boulton et al. 2009). The limited dispersal range of the CSSS suggests that restoring CSSS habitat adjacent to established subpopulations may be successful for supporting additional breeding pairs and encouraging population recovery.

4.3. Adult movements

Adult sparrows are primarily sedentary and show site fidelity to breeding areas (Dean & Morrison 2001, Lockwood et al. 2001). The overall area that a CSSS typically travels during its lifetime is under 50 ha (0.5 km^2; Pimm et al. 2002). The birds often stay within 1 km of their breeding area (Lockwood et al. 2001), and the areas used by adult sparrows during the non-breeding season overlap with their breeding season territories (Dean & Morrison 2001). Long-distance movements by adults are rare, generally shorter than the diameter of the average CSSS home range, and movements are terminated when birds reach the edge of short hydroperiod prairie habitat (Dean & Morrison 2001). For adult sparrows, the upper 5 and 10% of the distribution of movement lengths between locations were 362 and 276 m, respectively, and the longest-distance movement by an adult was 5.99 km (color banding and radio transmitter study; Dean & Morrison 2001). Movement data for adult birds indicate a mean distance of 277 m (n = 14; Pimm et al. 2002) and 212 m (n = 30; Lockwood et al. 2001) from the location where they were banded in the previous year. Males nested a mean distance of 40 m from the location of their nest in the previous year (n = 3), and nests from second clutches within the same breeding season were 8–95 m from the location of the first clutch (Lockwood et al. 1997). In some cases, males may make exploratory movements away from their breeding territory and on rare occasions relocate their territory, afterwards resuming sedentary movement behavior (Dean & Morrison 2001).

4.4. Conservation implications: territory, home range, movements

The sedentary behavior and limited movement patterns in the CSSS may impede colonization of newly suitable areas that are separated by unsuitable areas. Although marl prairie habitat has declined in spatial extent since the drainage and compartmentalization of the Everglades (Davis 1943, Pimm et al. 2002), restoration is expected to modify and increase habitat extent for the CSSS (RECOVER 2020). Increased water deliveries in the 1990s to the area of subpopulation A were followed by a decline in CSSS numbers and a shift towards unsuitable marsh vegetation communities (Curnutt et al. 1998, Nott et al. 1998, USFWS 2020). From 2019 to 2021, the maximum number of birds observed in subpopulation A in a given year was 4 adults (Virzi & Tafoya 2021). Restoration operations that will reduce water flows to the eastern side of subpopulation A from WCA 3A are expected to create more suitable breeding areas (RECOVER 2020, USFWS 2020). However, subpopulation A is the only subpopulation located west of Shark River Slough (Shark River Slough is a deeper-water area unsuitable for the CSSS). Thus, the viability of subpopulation A would likely depend on improbable long-distance movement events across Shark River Slough by sparrows from other subpopulations. Although rare, inter-subpopulation movements have been documented in the CSSS (Boulton et al. 2009, Virzi et al. 2009, Van Houtan et al. 2010). Portions of subpopulations C and areas southeast of subpopulations E and F may also become more suitable for the CSSS with restoration from changes in water operations that will increase water flows from Water Conservation Area 3A and 3B to the eastern side of Shark River Slough (RECOVER 2020). Owing to low dispersal, site fidelity, and sedentary behavior, the CSSS may not use these newly suitable areas even if they are more suitable than other existing areas (Dean & Morrison 2001).

Although some areas are expected to become more suitable for the CSSS, some areas of subpopulation D and the western areas of subpopulations E and F are expected to become less suitable from increased water deliveries (RECOVER 2020; for more information on expected future hydrologic conditions and recent trends, see Section 5), but birds may not move away from these areas to find more suitable areas. The low likelihood of sparrows re-colonizing or moving to areas as they become suitable may inhibit population persistence and recovery, and emphasizes the importance of maintaining consistency in habitat, and monitoring demographics and subpopulation trends over time.

5. THE FUTURE OF THE CSSS: POTENTIAL RECOVERY METHODS

5.1. Water operations

The Everglades is a managed ecosystem where water operations that transfer water from one compartment to another are continuously adjusted. Therefore, opportunities exist to create hydrologic conditions that support habitat and breeding conditions for the CSSS. The CSSS is just one of a suite of taxa of concern in the Everglades, and the natural system is just one component of restoration goals which aim to balance needs for flood control, drinking water, and the ecosystem (Sklar et al. 2005). However, water managers must consider the hydrologic needs of the CSSS to prevent the harm of individuals or habitat as stipulated under the ESA. Creating conditions for CSSS population recovery is critical as the population remains in peril.

With habitat loss and degradation identified as the major stressors to the CSSS (Walters et al. 2000), there are numerous measures that can aid in CSSS recovery given that hydrologic and habitat management are constantly implemented and evaluated in south Florida. Recovery of the CSSS may be achievable by reaching a rate of population increase (i.e. greater than zero) as a 3 yr running average for a minimum of 10 yr, and the maintenance of a minimum population of 6600 individuals for an average of 5 yr (USFWS 1999, 2010). Numerous actions are identified that can aid in CSSS recovery, including maintaining and avoiding the loss of habitat, implementing suitable water management regimes for the CSSS, eliminating the invasion of woody and non-native plants, monitoring the population and distribution of the CSSS, in-depth demographic monitoring, detailed ecology and habitat studies, and the development of a translocation protocol (USFWS 1999). Other potential actions include restoration of habitat west of Shark River Slough and in Taylor Slough, and the maintenance of 3 core breeding areas (subpopulations).

Adjusting water operations to allow for appropriate reproductive conditions during the CSSS breeding season may promote CSSS recovery, and may allow for other taxa to be prioritized at other times of year (Romañach et al. 2022). Research shows that double brooding in a given year is needed for the CSSS population to increase (Lockwood et al. 2001). The CSSS can raise a successful brood in approximately 40 d in the absence of detrimental nest flooding or fire (although between 30 and 60 d have been reported; Lockwood et al. 1997, 2001, Pimm et al. 2002). Therefore, it may be possible to manage the hydrology in CSSS habitat during the breeding season to provide conditions suitable for double-brooding and population increase.

The Combined Operational Plan (COP) was implemented in August of 2020 as a framework for system-wide water management in the Everglades (USFWS 2020) and includes consideration for CSSS habitat. Hydrologic conditions expected from the COP will affect the entire geographic range of the CSSS and are predicted to benefit the CSSS and the marl prairie habitat. In general, water operations under the COP will alter water deliveries from Water Conservation Areas 3A and 3B into Everglades National Park through water delivery structures that will decrease water flow to the area of subpopulation A west of Shark River Slough (which has become too wet for the CSSS) and increase water flow to the area east of Shark River Slough (where some areas have become too dry for the CSSS; Fig. 1). The COP is anticipated to provide conditions closer to the USFWS discontinuous hydroperiod target of 90–210 d for the CSSS and the USFWS dry nesting days target for the CSSS of 90 consecutive dry days during the breeding season between 1 March and 15 July (USFWS 2020). The ability to meet these targets may benefit the CSSS, including potentially increasing the duration of suitable breeding season conditions for subpopulations A and F, where areas of A will become drier and areas of F will become wetter (some areas of F showed hydroperiods shorter [drier] than the USFWS target, e.g. in 2003–2005; Sah et al. 2021). The areas of subpopulations B and C are not anticipated to experience major changes under the COP in meeting USFWS targets compared to existing conditions (USFWS 2020); however, some areas of subpopulation B may show decreased suitability (USFWS 2020). Additionally, mangrove encroachment is already reported in the southern areas of subpopulations B and D (Sah et al. 2020, Benscoter et al. 2021), indicative of increased salinity and vegetative shifts in these areas, and is likely to continue under sea-level rise (USFWS 2020). Areas of subpopulations D and E are anticipated to experience altered hydrology under the COP that may be less suitable for the CSSS, particularly for the western portion of subpopulation E. Areas used by subpopulation D may have reductions in the number of years that they meet the discontinuous hydroperiod target as a result of wetter conditions under the COP, although anticipated impacts are likely to be low. However, the range of subpopulation D is also affected by other water management and restoration activities, including the C-111 spreader canal project and upcoming Biscayne Bay and Southeastern Everglades Ecosystem Restoration project, which are both a part of CERP (USACE & SFWMD 2020). Subpopulation E, currently the second largest subpopulation, is expected to be the most impacted by COP, and it is anticipated that the CSSS use of E will shift toward the eastern side of the subpopulation's range as hydrology becomes wetter and less suitable for sparrows on the western side (USFWS 2020).

Anticipated changes under future hydrologic conditions are evaluated using several predictive models that can inform short and long-term resource management decisions regarding water operations. The CSSS Marl Prairie Indicator (MPI) estimates hydrologic suitability for the marl prairie vegetation community (values range from 0 to 100) using known historic locations with high CSSS presence (Pearlstine et al. 2016). Using the MPI, the potential hydrologic suitability of the marl prairie is shown for hydrologic water management scenarios such as the COP. The results of the CSSS MPI are in line with the predictions outlined in the COP Biological Opinion (USFWS 2020) regarding the potential effects of the COP hydrologic water operations on the CSSS and marl prairie habitat (Fig. 2), and in line with recent vegetation surveys conducted in CSSS subpopulations (discussed below; Sah et al. 2021). Improvements to marl prairie under the COP are expected in the northeastern area of subpopulation A and the area of subpopulation F. Minor improvements under the COP are expected in the areas of subpopulations B and C, with expected minor declines in suitability in the areas of subpopulations D and E. The MPI is also incorporated into the EverForecast application that simulates near-future water levels in the Everglades (Pearlstine et al. 2020) and models potential impacts on a suite of species and habitats (Haider et al. 2021b). EverForecast can be used by natural resource managers to evaluate trade-offs in a multi-species and habitat management context (Romañach et al. 2022) and can inform short-term decisions in water operations under the COP.

Vegetation surveys in CSSS subpopulations can aid in evaluating whether hydrologic conditions are suitable for supporting the freshwater marl prairie com-

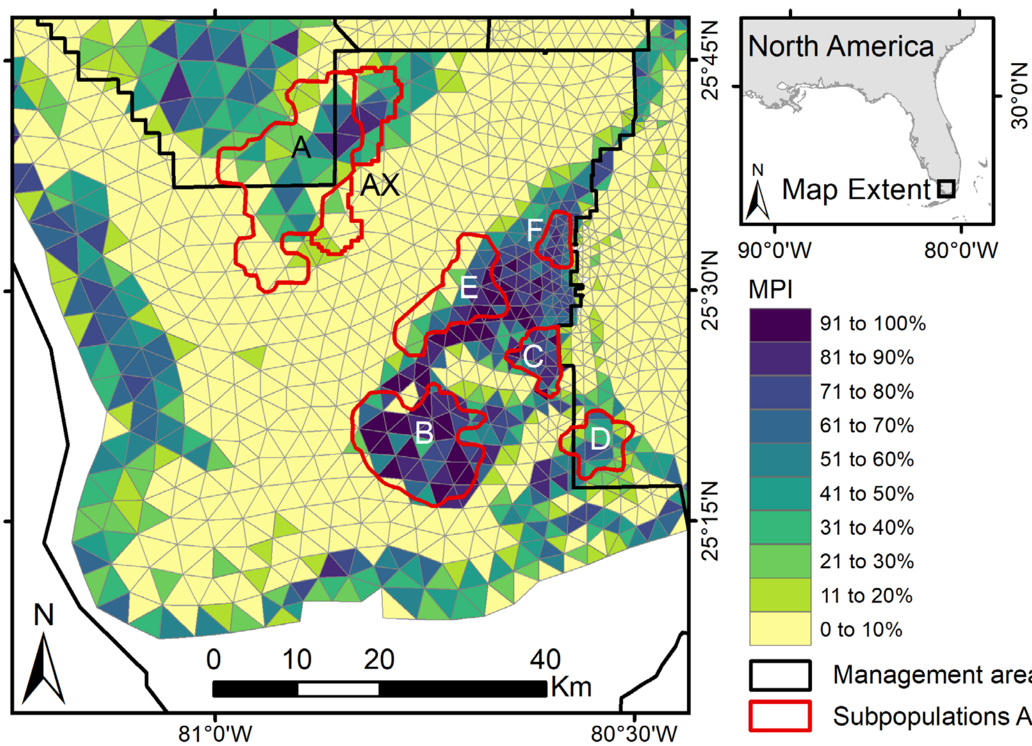

Fig. 2. Estimated hydrologic suitability for marl prairie vegetation using the Marl Prairie Indicator (MPI; Pearlstine et al. 2016) under the new Everglades water operations plan, the Combined Operational Plan (COP). The MPI ranges from 0–100, where higher numbers indicate greater suitability. The Cape Sable seaside sparrow (CSSS) comprises 6 subpopulations (A–F, where AX denotes expanded areas of subpopulation A on the eastern side identified as potential future suitable areas for the CSSS; USFWS 2020)

munity and the diverse set of taxa found there, including the CSSS. Vegetation surveys from 2017 to 2020 indicated that a drying trend already started in the northeastern portion of subpopulation A, where hydroperiods were within the USFWS target hydroperiod and vegetation shifted to a drier type (Sah et al. 2021). However, the western area of subpopulation A still showed hydroperiods longer than the USFWS target (Sah et al. 2021). Surveys located in subpopulation F showed a wetting trend in recent years (2017–2020), and hydroperiods within the USFWS target hydroperiod for most of the subpopulation. However, if hydroperiods continue to lengthen, there may be areas of subpopulation F that are too wet, such as on the western side owing to increased water delivery into Northeast Shark River Slough and on the eastern side from detention pond overflow (Sah et al. 2021, Gaiser et al. 2014). Vegetation surveys conducted in subpopulation E showed that mean hydroperiods were 37 d longer in 2017–2020 compared to 2003–2005, and the western side of E had hydroperiods that were longer than the USFWS target, indicative of a wetting trend in this subpopulation (Sah et al. 2021). Lastly, hydroperiods in the location of subpopulations B and C were 27 and 50 d longer in 2017–2020 compared to 2003–2005 (Sah et al. 2021). Continued monitoring can aid in determining if hydrologic conditions in these subpopulations change over time. Monitoring and assessment of ecological data using predictive tools can aid in understanding the effects of Everglades restoration on system components such as the CSSS and can aid in hydrologic management using the flexibility provided under the COP.

Other tools used in water management and restoration planning for the CSSS include the CSSS Viewer (USGS 2014), Sparrow Helper (see application in Beerens et al. 2016), EverSparrow (Haider et al. 2021a), and the Everglades Landscape Vegetation Succession (ELVeS) model (Pearlstine et al. 2011). In addition to the MPI, these tools allow scientists and mangers to input current or proposed hydrologic scenarios to generate output metrics related to suitable conditions for the CSSS or for CSSS presence or occupancy. The CSSS Viewer estimates real-time water depths in CSSS habitat, annual hydroperiods, and the proportion of area within each subpopulation that meets ≥40 and ≥90 consecutive dry days (USGS 2014). Sparrow Helper provides the proportion of area within each subpopulation that meets the USFWS target 4 yr discontinuous hydroperiod of 90–210 d. The EverSparrow model evaluates relationships among environmental variables and CSSS presence, and may be useful in evaluating the potential effect of changes in hydrology on CSSS presence (Haider et al. 2021a). The ELVeS model applies probabilistic relationships between vegetation community types and environmental variables to simulate spatially-explicit changes in vegetation community composition with changing environmental conditions, including that of the marl prairie habitat (Pearlstine et al. 2011). The use of predictive tools allows water managers to assess how hydrologic conditions are anticipated to impact species and habitats, which can inform potential adjustments to water management and restoration plans as a result.

5.2. Emergency actions: captive breeding, translocation

In addition to hydrologic and habitat management for the CSSS, emergency management actions, such as translocation, may be needed to recover the CSSS. Emergency management actions were identified in a plan to provide guidance and preparation and allow for immediate action to avoid unrecoverable population declines (Slater et al. 2009). These emergency management actions were not meant to be long-term solutions, stand-alone management actions, or conducted in isolation from other long-term recovery actions; rather, they were identified to supplement long-term actions in case of emergency (Slater et al. 2009). However, if habitat is degraded and long-term habitat recovery is not implemented and achieved, emergency management actions will likely either fail or only provide temporary recovery.

In the emergency management plan for the CSSS, there are a series of emergency threats, emergency actions, and decision framework trees to react to potential threats (Slater et al. 2009). Potential emergency threats include mismanagement of hydrology (identified as the most threatening trigger), disease, increased predation, and skewed adult sex ratio. The decision framework trees include criteria for determining whether an emergency management situation is present, protocol and methodology, cost estimates, monitoring needs to determine effectiveness, and other considerations. Emergency actions include habitat restoration, attracting the CSSS to suitable areas via conspecific attraction methods (e.g. song playback), predator control, nest protection, translocation, and captive breeding. For example, translocation is recommended before captive breeding in the emergency management plan. Due to limitations in producing self-sustaining populations, genetic risks for small populations, and high cost, captive breeding is considered an emergency action that is initiated only when all other conservation actions have failed, and is undertaken in conjunction with *in situ* actions that address the underlying causes of population decline (Slater et al. 2009).

Evaluation of whether translocation or captive breeding is feasible for the CSSS may include a risk analysis or population viability analysis to identify the point at which translocation is warranted for recovery, the subpopulation sizes that are needed to maintain viability of donor subpopulations, the age structure of individuals for translocation, and suitable locations for the release of translocated birds (Slater et al. 2009, USFWS 2019). Effective captive breeding, rearing, and release was accomplished for another endangered and endemic sparrow, the Florida grasshopper sparrow *Ammodramus savannarum floridanus* (USFWS 2019), which also provides lessons regarding the factors that may warrant captive breeding, rearing, and release of individuals and the methodology that accompanied successful captive breeding. Additionally, lessons from an unsuccessful captive breeding program for the extinct dusky seaside sparrow exist, where females that belonged to a separate mitochondrial DNA clade of seaside sparrows were bred and back-crossed with a limited number of male dusky seaside sparrows (only 5 males). The captive breeding program was discontinued after the last pure dusky seaside sparrow died, and the remaining hybrids died from predation or they escaped and presumably died (Zink & Kale 1995).

Another factor to consider when evaluating whether captive breeding and/or translocation of individuals is needed and feasible for population recovery is genetics. High levels of relatedness and evidence of inbreeding exist in some of the subpopulations (C. Beaver unpubl. data). However, there currently exists no evidence for Allee effects, or decreased fitness in subpopulations with lower population density (Gilroy et al. 2012). Additional genetic and demographic studies may provide information pertinent to the need and feasibility of translocation efforts for the CSSS.

6. CONCLUSIONS

The CSSS has a restricted range with many threats to its persistence, but water operations and ecosystem management may be able to aid in CSSS recovery, and potentially avoid emergency management actions such as translocation. Although the CSSS has limited dispersal ability, there is documented evidence of movement within and among subpopulations (Dean & Morrison 2001, Lockwood et al. 2001, Boulton et al. 2009). Adjustments to hydrologic conditions may promote increased habitat for the CSSS and may potentially result in colonization of suitable areas by subsequent generations. Four decades of research on this imperiled species indicate that habitat conditions with hydroperiods ranging from 90 to 210 d, at least 90 consecutive dry days during the breeding season, and fires during non-breeding every 5–10 yr provide conditions that may benefit CSSS recovery. In the Everglades headwaters to the north, the Florida grasshopper sparrow population declined by 89% over 20 yr to fewer than 35 breeding pairs across its range (Cox et al. 2020), but concerted conservation efforts led to reproduction of the subspecies. As for the Florida grasshopper sparrow, conservation, restoration, and habitat management actions may also provide steps toward recovery for the CSSS.

Water management decisions are made continuously in the Everglades to meet both immediate hydrologic needs for species and their habitats and for long-term restoration planning. Endangered species such as the CSSS receive special attention in water management decisions to avoid further harm to their populations and habitats. Understanding endangered species ecology can aid in deciphering how potential restoration actions may affect an endangered species, and how endangered species management fits into the broader context of multi-species and ecosystem-level management. Tools such as EverForecast can aid in optimizing water depths and distributions across the landscape for a suite of species and help decision makers prioritize water management for endangered species such as the CSSS during critical times of year or in critical locations (Romañach et al. 2022). This review provides information that can aid in CSSS recovery in the context of Everglades ecosystem-level restoration.

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