

COME HELL OR HIGH WATER: CONSERVATION OF THE FEDERALLY  
ENDANGERED CAPE SABLE SEASIDE SPARROW (*AMMODRAMUS MARITIMUS*  
*MIRABILIS*) IN THE DYNAMIC FLORIDA EVERGLADES

By

DAVID ANTHONY LA PUMA

A dissertation submitted to the  
Graduate School – New Brunswick  
Rutgers, The State University of New Jersey  
in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

Graduate Program in Ecology & Evolution

written under the direction of

Julie L. Lockwood

and approved by

Julie L. Lockwood, David Ehrenfeld, Peter J. Morin, and W. Greg Shriver

---

---

---

---

New Brunswick, New Jersey

January 2010

## **ABSTRACT OF THE DISSERTATION**

**COME HELL OR HIGH WATER: CONSERVATION OF THE  
FEDERALLY ENDANGERED CAPE SABLE SEASIDE SPARROW  
(*AMMODRAMUS MARITIMUS MIRABILIS*) IN THE DYNAMIC  
FLORIDA EVERGLADES**

By: David A. La Puma

Director of dissertation: Julie L. Lockwood

Understanding the effect of disturbance on rare and endangered species is critical for effective conservation. In this dissertation, I tested the effects of fire on the federally endangered Cape Sable seaside sparrow in Everglades National Park, Florida. In chapter 1, I used an unplanned fire event which burned a long-term research plot to test the effect of fire on the abundance and reproduction of a single subpopulation of the species. Sparrows were immediately impacted by the fire, in that no birds utilized the burned habitat for two full breeding seasons following the event. Moreover, no birds that had been banded in the burned habitat, prior to the fire, were ever relocated. Despite the initial impact, sparrows reclaimed burned habitat three years after fire at densities and nesting success indistinguishable from the unburned area. This suggests that fire provided neither benefit nor lasting negative effects to the sparrows. Vegetation structure was the most important factor in determining when sparrows return.

In Chapter 2, I determined whether the processes witnessed at the local scale were supported in patterns of sparrow occupancy across the entire range of the species. I used a 16-year fire history database in conjunction with 13 years of survey data on sparrow site occupancy to calculate time-since-fire for each survey point. Then using logistic mixed models, I tested whether fire had an effect on occupancy and whether this effect varied according to time-since-fire. My results indicate that sparrow occupancy was significantly lower at points that had experienced fire one and two years prior, but this effect was lost in points with three years or more since being burned. My results, therefore, provide the first confirmation of fire effects on the Cape Sable seaside sparrow at both the local and landscape scales.

In Chapter 3, I demonstrated how a long-term monitoring dataset, the 16-year sparrow helicopter survey, could be used to make inference about the statistical power of the current monitoring program. I used zero-inflated Poisson and binomial models to account for excess variation in the data, and generate parameter estimates from which I simulated sparrow population declines through time.

Using these simulated data, I determined the statistical power of the current sparrow survey to detect meaningful declines in both abundance and occupancy. My results showed that the current sparrow survey is unable to detect even large declines (>90%) over short time periods (three years). Survey power increased with additional years of data (5-10 years). With efforts to restore the Everglades ecosystem currently underway, park managers require a more precise tool than the current survey in order to detect important changes to sparrow populations.

## ACKNOWLEDGEMENTS

While I take full responsibility for any mistakes that may exist in this document, this dissertation would not have been possible without the support, encouragement, expertise, and manual labor of many people other than myself. Most of their names can be found in the acknowledgements for each chapter.

Julie Lockwood has been more than an advisor; she has been a friend, a confidant, and a mentor. From the field to the lab to the classroom, Julie has always led by example and for this I have the utmost respect. I only hope I have gleaned enough from watching her and working with her to become as successful a teacher and scientist as she is.

The Rutgers E&E faculty have been a constant source of inspiration and guidance during my time here. Specifically I must acknowledge the late Ted Stiles for introducing me to New Jersey, the Hutcheson Memorial Forest, and the idea that as scientists we must relentlessly question the natural world if we are ever to understand ecology and evolution. Peter Morin for being such a strong advocate for graduate students, and a wonderful teacher in the classroom. Only Peter could teach a multivariate statistics course, and everyone be smiling at the end of class. David Ehrenfeld, the esteemed conservation biologist turned curmudgeon, has both improved my ability to write, as well as my ability to see the forest for the trees. I will miss our conversations about peak oil and sea turtles, peppered with gardening advice and book recommendations. Greg Shriver, from the University of Delaware, has provided both, expertise on *Ammodramus* sparrows, and excellent insight into wildlife management.

Marsha Morin and Priscila Walsh deserve mountains of cash for their labor, but all I have to offer is this bit of sincere acknowledgement. They are the glue that keeps our



department together, along with a team of amazing office staff for whom we are all indebted.

Rick Lathrop and the entire staff at the Center for Remote Sensing and Spatial Analysis (CRSSA) have been instrumental in my progress. Jim Trimble specifically has provided me with tech support beyond the wildest dreams of a graduate student. The antics that unfolded within the center are legendary, and I will cherish those memories for years to come.

I feel extremely lucky to be a part of the Rutgers graduate community. Our graduate students are the best in their ability to carry out important research, and develop their skills to teach the next generation of students. To my extended family of graduate peers, thank you for being there for me when I needed you, and know I will always be there for you.

Finally, I must acknowledge my wife Inga Parker La Puma, who has stood by me through the many vicissitudes inherent in a graduate career. Always optimistic, always motivating, always beautiful and wonderful... how did I get so lucky. Her mark can be felt throughout this document, as she has been the critical alternate set of eyes when I have become too engrossed to see my own errors.

## **DEDICATION**

To Susan and Joseph La Puma, who made me who I am; and to the most beautiful women in my life, Inga and Corinna Wren, who continue to shape me as we grow together...

...and to the little brown bird; my Resplendent Quetzal of the Everglades; May our efforts prevail, and you always “chip-PANGGGG” across the wide prairies of Florida.

## TABLE OF CONTENTS

Title Page	i
Abstract of the Dissertation	ii
Acknowledgements	iv
Dedication	vi
Table of Contents	vii
List of Tables	viii
List of Figures	xii
Introduction	1
Chapter 1: Endangered species management requires a new look at the benefit of fire: The Cape Sable seaside sparrow in the Everglades Ecosystem	7
Chapter 2: Importance of fire for changes in Cape Sable seaside sparrow site occupancy in Everglades National Park, Florida	42
Chapter 3: Power to detect declines in occupancy and abundance in rare species: lessons from a long-term dataset	75
Concluding Remarks	122
Curriculum Vitae	136

## LIST OF TABLES

### CHAPTER 1

Table 1. Mean values ( $\pm$ SD) of the total number Cape Sable seaside sparrows 31  
detected at point count locations, Everglades National Park, 2002-2005. Sparrow  
density was lower for two years following fire in the burned area, returning in the  
third year to a level consistent with the unburned area.

Table 2. Overall nest survival probabilities for Cape Sable seaside sparrows 32  
based on daily survival estimates and calculated using the Logistic Mayfield  
Method (Hazler 2004). The overall nest survival probability represents the  
probability that a single nest will survive from the beginning of egg-laying until  
the fledging of the last nestling. The value is derived by raising the daily nest  
survival probability to the average number of days in the nesting cycle. In the  
case of the CSSS, there are 12 egg days, up to 4 hatching days, and 9 nestling  
days for a total of 25 days. The overall nest survival probability in the unburned  
area remains relatively consistent over the study. In 2002 we witnessed a  
decrease in nest survival, most likely due to a water pumping station which went  
into operation during the breeding season. After two seasons of exclusion from  
the burned plot, the 2004 and 2005 survival probabilities for those birds that  
recolonized the area was indistinguishable from pre-fire levels.

Table 3. Pairwise Analysis of Similarity (ANOSIM) results for vegetation species composition (live only) between burned (B) and unburned (U) transects, one-month (0), one-year (1), two-years (2), and three-years (3) post fire. Results are from Mote Carlo simulation of 10000 permutations. 33

Table 4. Eigenvector loadings for Principal Component Analysis. Values above 0.35 were deemed important and used in describing each Principal Component axes. Principal Component 1 (PC1) represents a measure of *Cladium jamaicense* seedhead height and seedhead density. Principal Component 2 (PC2) represents the amount of exposed bare ground, and amount of standing dead cover. 34

## CHAPTER 2

Table 1. Area (in hectares) of spatial extent burned (SEB) and total area burned (TAB) for each population from 1989 – 2005 (see text for definitions). Also included are the percentages of the total geographical extent of each population that burned calculated using SEB or TAB, given both as annual estimates and over the entire period of record. 67

Table 2. Univariate models for the relationship between Cape Sable Seaside Sparrow site occupancy one-year post-fire and four characteristics of the fire. Categorical estimates for fire type and season are interpreted as relative to ‘Prescribed’ burns and ‘Wet’ season respectively. Linear estimates were 68

produced from a binomial logistic mixed model that included year and controlled for nested population structure as random effects.

### CHAPTER 3

Table 1. The relationship between statistical power and associated errors of omission (type II) and commission (type I). The question mark is a reminder of the uncertainty always inherent in hypothesis testing. After Mapstone (1995) 103

Table 2. Parameter estimates for each subpopulation from the best-fit zero-inflated Poisson model ( $\lambda_{2007}$ ,  $\theta_{ZIP}$ ), the logistic regression ( $\psi$ ), as well as our heuristic estimates of zero inflation ( $\theta_{ZIB}$ ) for site occupancy. Lambda values are for the year 2007, which allows for simulating population declines into the future. Estimates are used to simulate population estimates of abundance and occupancy over various scenarios of population decline. 104

Table 3. Results of fitting 16 years of sparrow survey count data to a series of zero-inflated Poisson models with year and subpopulation as regressors for the number of sparrows counted, and subpopulation as a regressor for zero-inflation. 105

Table A.1. Results from large subpopulation (B) occupancy analysis to derive estimates of detection probability. Data are from 147 sites surveyed at least six times each between 1996 and 2007. Models with constant detection and survey-specific detection were considered. 106

Table A.2. Results from small subpopulation (C) occupancy analysis to derive 107  
estimates of detection probability. Data are from 15 sites surveyed five times in  
2007. Models with constant detection and survey-specific detection were  
considered.

## LIST OF FIGURES

### CHAPTER 1

- Figure 1. Map showing South Florida coastline with Everglades National Park boundary. Crosshatched areas represent extent of Cape Sable seaside sparrow habitat. The Lopez fire (solid black) is shown originating from the eastern boundary of the park, and extending westward, bisecting a subpopulation of the sparrows. Inset: Detail of the Lopez fire (solid black) and our 2 km x 1 km study plot (hatched rectangle). 37
- Figure 2. Three theoretical scenarios of the effect of fire on *A. m. mirabilis*. The horizontal dashed line represents the control plot, where no change is occurring. After fire, each scenario is predicted to show a drop in a measured parameter, which in our case would be either sparrow density or nesting success. This condition is expected to continue for some period of time, at which point the burned habitat will show either a measurable degradation due to fire (C), no effect of fire (B), or enhancement by fire (A). Our time scale is based on previous research by Pimm et al. (2001), and work by Werner (1975) and Taylor (1983). 38
- Figure 3. The daily probability of survival for nests of *A. m. mirabilis* calculated for each year in both the unburned area (solid line with open squares) and burned plot (dashed line with solid triangles) ( $\mu \pm 95\%$  CI). 39



Figure 4. Non-metric Multi Dimensional Scaling (NMDS) ordination for *A. m.* 40  
*mirabilis* habitat composition. Each symbol represents a single plot. Data is  
divided by treatment and time since fire; one month (triangles), one year  
(inverted triangles), two years (circles) and three years (squares). Open symbols  
represent vegetation plots in the burned treatment (n = 22) and solid symbols  
representing those in the control (n=22). This ordination indicates very little  
compositional different between treatments and time-since fire, supporting the  
idea that composition recovers quickly following fire.

Figure 5. Principal Component Analysis (PCA) for *A. m. mirabilis* habitat 41  
structure. As above, each symbol represents a single plot. Data is divided by  
treatment and time since fire; one month (triangles), one year (inverted triangles),  
two years (circles) and three years (squares). Open symbols represent vegetation  
plots in the burned treatment (n = 22) and solid symbols representing those in the  
control (n=22). Segregation is evident after the first month post fire,  
characterized by shorter vegetation, fewer *Cladium jamaicense* seedheads, more  
bare ground, and less dead cover. In each successive time period, the burned  
plots increase convergence toward the control, but are noticeably slower on the  
PC1 axis than on the PC2, as bare ground is recovered sooner than vegetation  
height.

## CHAPTER 2

Fig. 1. Map of Everglades National Park in south Florida, showing locations of 71

six extant populations of the Cape Sable Seaside Sparrow (area with diagonal line fill), and perimeter of fire within population E that was studied by La Puma et al. (2007; white with black outline).

Fig. 2. The frequency with which range-wide survey points, that have ever held sparrows, have burned up to four times during the period of record (1989 – 2005), by population. Population A has the fewest burned points, whereas D and F have the greatest proportion of points that burned more than twice. 72

Fig. 3. Probability of site occupancy by Cape Sable Seaside Sparrows following known fire events during the 16 years ranging from 1989 – 2005. Error bars around each estimate are +/- 1 SE and were calculate using the Delta method to back-transform estimates. The dotted line is the average site occupancy for all frequently surveyed points (i.e. those surveyed at least six times), which are known to have been occupied by sparrows (i.e. have had at least on sparrow detection) and have never burned during the study period. The fitted line is the logistic quadratic  $P(\Psi) = -1.83 + 0.20TSF + -0.01TSF^2$ . 73

Fig. 4. Probability of site occupancy by Cape Sable Seaside Sparrows in annual range-wide surveys following known fire events for a) the small populations (A = solid square, C = hollow square, D = hollow triangle, F = hollow diamond) and b) the large subpopulations (B = solid square, E = hollow square). Because of differences in fire frequencies between populations, time-since-fire was binned into four successive intervals. Occupancy increases over the first two bins in all populations except A (see results). In populations B (estimate  $\pm$  std err =  $0.55 \pm 0.20$ ,  $t = 2.74$ ,  $P = 0.006$ ), C (estimate  $\pm$  std err =  $2.05 \pm 1.00$ ,  $t = 2.05$ ,  $P = 0.041$ ), and E (estimate  $\pm$  std err =  $1.16 \pm 0.46$ ,  $t = 2.54$ ,  $P = 0.011$ ) these increases are significantly greater in the second interval of time-since-fire over the first. The average trends in occupancy (excluding population A) are quadratic models for time-since-fire across the entire survey period plotted at the midpoint of each of the four bins. All models control for the effect of year and quad (see methods).

### CHAPTER 3

Figure 1. Map of Cape Sable seaside sparrow habitat in Everglades National Park, Florida USA. Subpopulations are labeled A-F. The “large” populations are B and E, while the “small” populations are A, C, D, and F.

Figure 2. Histogram of point count values for the total population of the Cape Sable seaside sparrow (1992-2007).

Figure 3. Histograms of point count results for each subpopulation of the Cape 118  
Sable seaside sparrow (1992-2007). Subpopulations A, C, D & F are considered  
“small”, whereas B and E are the only remaining “large” subpopulations.

Figure 4. A schematic of the zero-inflated Poisson simulation. This simplified 119  
figure illustrates the idea of a zero-inflated Poisson model consisting of two joint  
distributions. Essentially, the values generated via the Poisson distribution (using  
a value for  $\lambda$ ) are multiplied by those generated via the binomial distribution  
(using a value for  $\theta$ ) to arrive at a final dataset of zero-inflated values.

Figure 5. Power to detect a 3, 5, and 10-year decline in sparrow abundance. Open 120  
symbols represent individual subpopulations, while the closed symbol represents  
the total population. The horizontal line represents the power threshold of 90%.

Figure 6. Power to detect a 3, 5, and 10-year decline in sparrow occupancy. Open 121  
symbols represent individual subpopulations, while the close symbol represents  
the total population. The horizontal line represents the power threshold of 90%.

## INTRODUCTION

The Seaside Sparrow (*Ammodramus maritimus*) is an inconspicuous passerine of salt and brackish marshes. It occurs in patches of marsh from the coast of New Hampshire down the east coast of Florida, and along the Gulf coast of Florida to the southeast tip of Texas (Post and Greenlaw 1994). Of the extant subspecies of the seaside sparrow, the Cape Sable seaside sparrow (*A.m. mirabilis*) is the only one known to occupy freshwater marshes dominated not by *Spartina* sp., but by a diverse array of herbaceous plants such as *Muhlenbergia filipes* M.A. Curtis and *Cladium mariscus* (L.) Pohl ssp. *jamaicense* (Crantz) Kük. (Lockwood et al. 1997). The Dusky seaside sparrow (*A.m. nigrescens*), which historically occurred along the St. John's River, and the area that is now occupied by Cape Canaveral, was the only other subspecies to occupy freshwater prairies. The Dusky seaside sparrow was the most recent taxon in the United States to go extinct, which it did in 1990 (Walters 1992). It is with this fact in mind that I set out to conduct research on the federally endangered Cape Sable seaside sparrow.

The Everglades ecosystem is one of paradoxes. At first glance, it is difficult to discern that the landscape is in constant motion. In fact, to many the Everglades appear more like a swamp, than a "river of grass", as dubbed by the late Everglades advocate, Marjory Stoneman Douglas (Douglas 1974). The ecotones within this river of grass are dictated by a combination of the underlying micro topography and abiotic effects of seasonal rainfall, periodic fires, and the occasional hurricane (Davis and Ogden 1994). Water and topography determine the ecological gradient from low-lying marshes to upland forest, while fires prevent the conversion of pine rocklands (dominated by the endemic *Pinus elliottii* Engelm. var. *densa* Little & Dorman) to fire-susceptible subtropical hardwood hammocks. Over

millions of years, with the co-mingling of periodic disturbance and seasonal patterns of precipitation, what we know as the Everglades mosaic has been created.

The proximity of the Everglades to the major metropolitan City of Miami has resulted in significant modifications to the ecosystem over the last hundred years. Efforts to divert water for agriculture, drain and fill wetlands for development, and erect highways to traverse the great landscape, have lead to many impacts on the ecosystem's ability to function. Not the least of these effects has been felt by the diverse suite of wildlife, which had evolved to exist in a dynamic landscape with specific constraints, only to have new dynamics imposed on it in a fraction of the time it took for the Everglades to develop. For instance, the Everglades Snail Kite (*Rostrhamus sociabilis plumbeus*), a highly specialized hawk that feeds almost exclusively on the freshwater apple snail (*Pomacea paludosa*), is currently on the brink of extinction due to modifications to the natural Everglades hydrology (Martin et al. 2006). Like most organisms in this system, the hawk's persistence is contingent on multiple trophic levels and linkages between the abiotic water flows which support the habitat necessary for its food to thrive, periodic droughts which result in the dead vegetation necessary for nest building, and the source populations of its primary food. Catering to the needs of neighboring development has meant pumping water into, or out of, the Everglades to prevent suburban flooding, or to provide water to the ever-growing metropolitan population. These engineering feats have come at the expense of disrupting the delicate hydrologic cycle within the park boundaries.

The Everglades have changed drastically since the first canals were dug in the early 1900s. Impacts range from saltwater intrusion due to rerouting of fresh groundwater (Ewe et al. 2007), to the introduction of many invasive trees including the fire-tolerant and water

demanding *Melaleuca quinquenervia* (Cav.) S.F. Blake (Dray et al. 2006). The most recent threat, the explosion of the Burmese python (*Python molurus*) appears to be consuming everything from white-tailed deer (*Odocoileus virginianus*) to the Federally Endangered Key Largo wood rat (*Neotoma floridana smalli*) (Snow et al. 2007).

In response to overall degradation of the Everglades ecosystem, a concerted effort is underway to restore water delivery to Everglades National Park. Everglades management hopes that by getting the water flowing correctly, the flora and fauna will respond in kind. It is an ambitious goal, which carries with it one of the largest financial and most bi-partisan political backings of any ecosystem restoration project in the world. As such, the effects of a project of this magnitude must be carefully monitored to ensure that short-term impacts to threatened or endangered species are efficiently mitigated to prevent loss of biodiversity. In order to do so, we must understand the effects of disturbance on these species, realize their tolerances, and develop metrics with which to monitor their response to restoration as it occurs.

My dissertation focuses on the conservation and management of one such species, the federally endangered Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*). Specifically my research attempts to understand the relationship between this species, and the fire regime that characterizes the freshwater marl prairies it calls home. In Chapter 1, I took advantage of an unplanned fire event which burned over 3000 hectares of occupied sparrow habitat during the 2000 breeding season. Because of the preexisting data available from this site, I was able to conduct a before-after/control-impact study to directly test the effect of fire on sparrow nest success and abundance, as well as habitat structure and composition. Results from this study lead me to wonder whether the effects I detected were site specific, or could

be generalized to the landscape. To answer this question, I developed a fire history geodatabase that included all fires within Everglades National Park from 1984 through 2005.

In Chapter 2, I used this geodatabase in conjunction with 16 years of sparrow survey data to test whether the processes I had identified at the local scale were reflected in the patterns across the entire landscape. I used a mixed model logistic regression to test whether 1) fire had an effect on occupancy, 2) whether attributes of the fires could explain variation in occupancy after fire, and 3) whether I could detect any trends in occupancy across annual time-since-fire categories for up to 13 years following fire.

Understanding the effects of disturbance on an endangered species is critical to effective management and conservation. In light of the Comprehensive Everglades Restoration Plan (CERP), I was interested in whether the current sparrow survey could provide information necessary for park managers to detect impacts to the species due to restoration actions. In Chapter 3, I used a novel approach to test the power of the current survey to detect population declines of various magnitudes over biologically important time periods. In doing so I have developed a simulation program which can be used by park management to evaluate the benefit of adjusting the sparrow survey in an effort to improve the overall statistical power.

Each of the three main chapters of my dissertation was written as a stand-alone manuscript for publication in peer-reviewed journals. As such, they are formatted differently to reflect the journal requirements. Additionally, each chapter is written in first-person plural to indicate that they were written with my dissertation advisor, Julie Lockwood (chapters 1,2 & 3), our field supervisor Michelle Davis (chapter 1), and my two wonderful collaborators,



Phillip Cassey (chapter 2) and Kenneth Elgersma (chapter 3). Chapter 1 was published in the journal *Biological Conservation* in 2007; I intend to submit Chapter 2 to *Ecological Applications*, and Chapter 3 will go to the journal *Bird Conservation International*.

Following Chapter 3 are a series of management recommendations based on my findings. It was my experience reading “A Shadow and a Song”, the story about the demise of the Dusky seaside sparrow, which originally inspired me to pursue this research. For that reason, and for the myriad reasons that have presented themselves since the Lopez fire roared across subpopulation E, it is my sincerest hope that my management recommendations will aid in the recovery of the Cape Sable seaside.

## LITERATURE CITED

- Davis, S.M., Ogden, J.C., 1994. Everglades : the ecosystem and its restoration. St. Lucie Press, Delray Beach, FL.
- Douglas, M.S., 1974. The Everglades : river of grass, Rev. edn. Mockingbird Books, Atlanta.
- Dray, F.A., Bennett, B.C., Center, T.D., 2006. Invasion History of *Melaleuca quinquenervia* (Cav.) S.T. Blake in Florida. *Castanea* 71, 210-225.
- Ewe, S.M.L., Sternberg, L.S.L., Childers, D.L., 2007. Seasonal plant water uptake patterns in the saline southeast Everglades ecotone. *Oecologia* 152, 607-616.
- Lockwood, J.L., Fenn, K.H., Curnutt, J.L., Rosenthal, D., Balent, K.L., Mayer, A.L., 1997. Life history of the endangered Cape Sable seaside sparrow. *Wilson Bulletin* 109, 720-731.
- Martin, J., Nichols, J.D., Kitchens, W.M., Hines, J.E., 2006. Multiscale patterns of movement in fragmented landscapes and consequences on demography of the snail kite in Florida. *Journal of Animal Ecology* 75, 527-539.
- Post, W., Greenlaw, J.S., 1994. Seaside Sparrow (*Ammodramus maritimus*), In *The Birds of North America Online*. ed. A. Poole. Cornell Lab of Ornithology, Ithaca.
- Snow, R.W., Brien, M.L., Cherkiss, M.S., Wilkins, L., Mazzotti, F.J., 2007. Dietary habits of the Burmese python, *Python molurus bivittatus*, in Everglades National Park, Florida. *Herpetological Bulletin* 101, 5.
- Walters, M.J., 1992. A Shadow and a song. Chelsea Green Publishing, Post Hills.

Chapter 1

**ENDANGERED SPECIES MANAGEMENT REQUIRES A NEW LOOK  
AT THE BENEFIT OF FIRE: THE CAPE SABLE SEASIDE SPARROW  
IN THE EVERGLADES ECOSYSTEM**

David A. LA PUMA<sup>a1</sup>, Julie L. LOCKWOOD<sup>a\*</sup>, and Michelle J. DAVIS<sup>a,2</sup>

<sup>a</sup> Department of Ecology, Evolution and Natural Resources, Rutgers University, 14 College Farm Rd., New Brunswick, New Jersey, 08873, USA

\* Corresponding author: Tel.: +00 1 732 932 9336; fax: +00 1 732 932 8746

Email addresses: [lapuma@eden.rutgers.edu](mailto:lapuma@eden.rutgers.edu) (D.A. La Puma), [lockwood@aesop.rutgers.edu](mailto:lockwood@aesop.rutgers.edu) (J.L. Lockwood), [vireoojorojo@hotmail.com](mailto:vireoojorojo@hotmail.com) (M.J. Davis).

<sup>1</sup> Tel.: +00 1 732 932 3313

<sup>2</sup> Tel.: +00 1 305 258 3791

# **ENDANGERED SPECIES MANAGEMENT REQUIRES A NEW LOOK AT THE BENEFIT OF FIRE: THE CAPE SABLE SEASIDE SPARROW IN THE EVERGLADES ECOSYSTEM**

## **ABSTRACT**

Although disturbance processes play important roles in maintaining habitat heterogeneity, the potential effects of such processes on rare or endangered species is virtually unknown and difficult to test. We use an unplanned fire, which burned half of a long-term study plot, as a natural experiment to test the effects of fire on the federally endangered Cape Sable seaside sparrow in Everglades National Park. By implementing a Before-After-Control-Impact study design we determine the mechanistic link between fire and demography of this endangered sparrow. Our results show that while the sparrow tolerates fire, neither sparrow density nor nesting success are enhanced by fire, which runs contrary to the current paradigm in which sparrows are expected to benefit and therefore require fire for persistence. Our results caution against the assumption that occupancy of disturbance-prone habitat automatically suggests dependence on disturbance. Land managers must prevent large and frequent fires from burning occupied sparrow habitat to best manage for the species. Moreover, it is imperative that more studies focus on the effects of disturbance processes on rare and endangered species in order to prevent further loss of biodiversity.

## **KEYWORDS:**

## INTRODUCTION

Disturbance often plays an important role in maintaining habitat heterogeneity (Askins 2002; Brawn et al. 2001; Pickett and White 1986; Sousa 1984), and in many cases this heterogeneity must be sustained for select species to persist (Madden et al. 1999; Tucker et al. 2006), whether being directly responsible for the substrate required by an organism for survival or the creation of multiple habitat types that satisfy the diverse needs of a particular organism (Law and Dickman 1998; Moran-lopez et al. 2006). However, when the species of concern is threatened with extinction even natural disturbance events must be viewed with caution. Such populations are by definition low in numbers and often restricted to small areas of suitable habitat. Thus, disturbance events may drive the population to extinction even if the event is precipitated by natural causes and despite the fact that the disturbance may be required to maintain or create suitable habitat (Jakalaniemi et al. 2006). For this reason there is a critical need to understand how species threatened with extinction respond to disturbance events so that these events can be managed (as much as feasible) to ensure recovery. Despite this need there are remarkably few studies that follow the effects of disturbance on any species in natural environments, much less endangered vertebrates (Whelan et al. 1995).

Here we provide information on the demographic response of an endangered bird, the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), to an unplanned fire that swept through its habitat within the Florida Everglades ecosystem. Our results illustrate the complexity of managing an endangered species within dynamic ecosystems, and the value of testing the assumption that such species rely on disturbances events for their long-term persistence.

The Cape Sable seaside sparrow has been protected under the United States Federal Endangered Species Act since the act's inception in 1973. This non-migratory subspecies is geographically restricted to six subpopulations, almost all of which are located within the borders of Everglades National Park (ENP) and Big Cypress National Preserve of South Florida, USA (Figure 1). The sparrow lives exclusively in short hydroperiod (< 7 months of standing water) freshwater marl prairie. This ecotype, although extensive, is not contiguous sparrow habitat. Slight decreases in elevation allow for the formation of marsh, whereas slight increases in elevation allow for the emergence of pines and upland hardwoods. Work by Jenkins et al. (2003a; 2003b) showed that the sparrows avoid habitat within 40m of emergent pine or hardwood vegetation. Likewise, sparrows avoid habitat that is too wet, as it does not provide the necessary structure for nesting or foraging (Lockwood et al. 2001). Therefore, sparrow habitat is limited to a subset of the total marl prairie community, that which is free of emergent vegetation and has a drydown period during the peak breeding season from early March through May.

Overlain across this landscape is the effect of fire (Lockwood et al. 2003). There are multiple feedbacks between water flows, vegetation, soil type and fire in the Everglades that creates a complex temporal and spatial burn pattern (DeAngelis and White 1994; Lockwood et al. 2003). In their fire history analysis of the Everglades from 1948 through 1992, Gunderson and Snyder (Gunderson and Snyder 1994) outlined temporal fire patterns for the entire ecosystem. They found that fires consumed large areas (annual geometric mean  $>93\text{km}^2$ ) of the Everglades about every 10 to 15 years, and these large fires were followed by years of significantly smaller total area burned. Most natural fires occurred during wet season thunderstorms typical of June and July, however very large fires occurred during May

when the conditions were still relatively dry, and intensified in El Nino years (Beckage et al. 2003; Gunderson and Snyder 1994). This naturally variable fire return interval is further complicated by the effects of incendiary fires (i.e. arson and escaped agricultural burns) and fire management practices. Everglades National Park, and other land-holding public agencies, actively pursue the use of fire as a management tool for maintaining early successional plant communities and controlling invasive plant species. Additionally, incendiary fires result in the wildland-urban interface burning both more often, and more out of season, than what is considered natural (Lockwood et al. 2003). Each of these human-derived sources of fire in the ecosystem has a spatial and temporal signature that is distinct from more natural fires. Prescribed burns tend to produce more frequent and smaller fires than those ignited by lightening, whereas incendiary fires burn a significantly larger ( $>2\times$ ) area and greater frequency than natural fires due to their concentration during the driest months (Gunderson and Snyder 1994).

We know from previous work (Taylor 1983; Werner 1975) that fire removes all standing vegetation within sparrow habitat making it unsuitable for some period of time and creates a complex burn pattern that may contribute to the spatial segmentation of the sparrow population. However, it is not clear how long the effects of fire last, whether fire is needed to ‘re-set’ the habitat so it remains suitable for sparrows over the long-term, or how sparrow dispersal dynamics interplay with the spatial extent of fires to influence subpopulation recovery or metapopulation persistence.

In Figure 2 we outline three possible scenarios of how fire may impact the sparrow population based on our understanding of the species and previous work (Pimm et al. 2002; Taylor 1983; Werner 1975). In all three cases we expect the dependent variable (i.e. some

measure of sparrow population size or demography) to be reduced immediately following fire and persist in a reduced state for at least one breeding season. In scenario A, where habitat is enhanced by fire, the measure of sparrow demography within the fire-impacted site returns and exceeds that measured in the control. In the case where fire has no effect (B), the demographic features of the burned site return to levels indistinguishable from the control. Finally, if fire has a negative effect (C), we expect demographic rates within the burned site to persist at levels significantly below the control. We compare our results from below to these competing models thereby deducing which scenario predominates for Cape Sable seaside sparrows.

## **METHODS**

On May 8, 2001 a human-ignited fire (hereafter the Lopez fire) began at the eastern boundary of Everglades National Park (Figure 1). Over the course of fifteen days the Lopez fire burned 3,410 ha until controlled on May 23, 2001. Given the dry conditions at the time, the fire consumed the great majority of vegetation in its path, leaving little unburned. The Lopez fire represents an early season fire event that would not be characteristic of an average fire season. However, the Lopez fire does fall well within the range of fires over the period of record provided by Gunderson and Snyder (1994) and such fires may be expected to occur more frequently given the altered water flow regime currently affecting the northeastern portion of Everglades National Park (Lockwood et al. 2003).

The path of the fire included the southern portion of subpopulation E of the Cape Sable seaside sparrow, including the southern edge of a four-year old study plot originally designed to document demographic parameters of this population (Figure 1). Thus our study



plot is 2 km by 1 km (200 ha; see Figure 1 inset) and contains 60% (120 ha) unburned habitat (hereafter referred to as the control plot) and 40% (80 ha) burned habitat (hereafter referred to as the burned plot). This situation allowed us to utilize a Before-After, Control-Impact (BACI) design, which allows more precise inferences on the effect of fire on sparrow demography (Manly 2001).

### *Sparrow Density*

In order to document changes in sparrow density due to the fire, we established 15 permanent point count locations distributed systematically across the entire study plot. Each point was visited eight times per breeding season. The number of sparrows seen or heard within a 200m radius was recorded over a 5-minute interval. The time of day was held constant at between 0700 and 0900, although the order in which point counts were visited was varied to correct for any unforeseen time-dependent variance. Our survey points, being located at 400m intervals across the site, therefore ensured near complete coverage of the plot.

Using ArcGIS (ESRI 2005) we classified each point count location as either burned, edge or control by placing a buffer of 200m diameter around each point and superimposing the buffered points on the perimeter of the fire scar. All points with a buffer >75% in either the burned or control plot were assigned accordingly, whereas any point with a buffer of 25-75% burned was classified as edge. This resulted in a final distribution of eight points in the unburned area, three points on the edge of burned and unburned, and four in the burned area. Because we return to the same point count stations each year, and the Cape Sable seaside sparrow shows significant site fidelity (Pimm et al. 2002), we cannot assume that our point counts are independent of each other between years. Therefore we used a repeated measures

multivariate analysis of variance, or MANOVA (SAS for Windows v.9), to analyze our point count data with burned, edge, and control as our treatment levels and year as our repeated measure factor. To determine the polarity of any detected differences, we performed a comparison of least square means with the Bonferroni correction for multiple comparisons. A post-hoc comparison of means between the 2002 and 2004 points in the control plot was used to test for significance of observed differences between the two years.

### *Dispersal*

Since 1998 we have color banded 383 Cape Sable seaside sparrows within our study plot, 156 of these were banded as adults and the remainder as first year juveniles (i.e. hatched during the breeding season in which they were banded). Color bands allow us to identify individuals and confirm their survival and breeding location without the need to recapture them. Because we marked adult and juvenile sparrows with color bands since 1998, we can document which individuals survived the fire and the origin of individuals that recolonized the burned area. We began looking for banded individuals one-month post-fire and have since surveyed the burned plot annually to see if individuals from the control plot recruit to this site. Because we systematically search outside of our study plot for banded birds, all unmarked individuals that recruit to the plot are assumed to have dispersed from locations further than 200m.

### *Daily Probability of Nest Survival*

A key demographic parameter that indicates the likelihood of Cape Sable seaside sparrow population persistence is nesting success (Lockwood et al. 2001). Thus, we estimated daily

probability of nest survival and how this probability was affected by fire. Nests were located by observing parental behavior, and were marked and monitored until fledging or failure. If nests were found empty, the area was observed for signs of fledged young, including parental activity away from the nest and the sound of fledgling–parent communication. We used the Logistic Mayfield method for calculating daily probability of nest survival with 95% confidence limits (Aebischer 1999; Hazler 2004). Logistic Mayfield is an extension of the traditional Mayfield method (Mayfield 1975), which treats each day of nest observation (exposure day) as a binomial trial. The daily probability of survival is then raised to a power equal to the number of days in the nesting cycle (in our case that number is 25; Lockwood et al. (1997) resulting in the total probability of a nest surviving the nest cycle. Because we have data on 20 nests prior to the Lopez fire ( $n = 7$  in the burned plot,  $n = 14$  in the control) we first calculated the daily probability of nest survival for these two groups to test for site-specific differences prior to the fire, as well as to provide a baseline with which to compare the post-fire data. We then calculated the daily probability of nest survival for the control and burned plot from 2002 – 2005 inclusive.

### *Vegetation Composition and Structure*

If fire has a positive effect on sparrow density and nesting success, the mechanism likely lies within the vegetation dynamics initiated by the physical removal of vegetation and deposition of minerals post-fire. From previous work we know that vegetation structure plays a large role in determining where Cape Sable seaside sparrows place their nests and how successful these nests are (Pimm et al. 2002). Thus, in June 2001 (i.e. one month post-fire) we established one vegetation transect per treatment (control, burned) across our study plot.

Each transect ran the length (east-west) of the plot. We systematically placed two 1m<sup>2</sup> quadrats every 200m along these lines and collected 22 vegetation samples along each east-west transect. The variables measured included percentage cover of each live plant species, as well as the percentage cover of all dead vegetation (not separated by species) and bare ground. Structural variables included the height of the tallest grass, the height and number of sawgrass seedheads, and the effective height of ground cover. All vegetation variables have been collected and analyzed prior to this study and found to be important elements of sparrow habitat (Pimm et al. 2002).

For analysis of compositional data we used the multivariate software Primer-E®, and initially calculated the full Bray-Curtis species similarity matrix for all samples as compared to all others regardless of time since fire. We then used this matrix as the basis for constructing a compositional similarity graph using non-metric multidimensional scaling (NMDS) (Clarke and Warwick 1994). The sample sites are the species compositions of each transect (burned or control) divided into four ‘time since fire’ categories; one-month post fire, one-year post fire, two-years post fire, and three-years post fire. Thus, in producing an NMDS plot, we are evaluating how the composition of the burned and control transects have changed since the time of the fire. The 22 positions of the points in the NMDS space can illustrate the extent to which the vegetation composition of the burned transect has recovered as measured by its similarity to the control transect. In addition, because the control transect has been measured across four successive years, we gain an understanding of the degree to which vegetation composition naturally varies from year to year within sparrow habitat. We then used the analysis of similarity (ANOSIM) function within Primer-E to evaluate whether or not the two transects differed significantly with respect to their relative similarities. We

conducted 10,000 random permutations to produce a distribution of  $R$ -values for comparison to the overall, or global, observed  $R$ -value.

For analysis of structural variables we used Principal Components Analysis (PCA) (Reyment et al. 1984). Sample quadrats were again grouped by transect (burned, control) and further divided by time since fire (one-month, one-year, two-years, three-years). The first two Principal Components were retained as they accounted for the majority of the observed variance between sample quadrats (66%). We used repeated measures MANOVA (SAS for Windows v.9) for each principal component score (PC1 and PC2) associated with the 22 samples, and a comparison of least square means to determine at what point the difference between the control and impact transects became insignificant.

## RESULTS

### *Sparrow Density*

After the Lopez fire, Cape Sable seaside sparrows were absent from the burned plot for the remainder of 2001, as well as for the 2002 and 2003 breeding seasons (Table 1). Using a simple comparison of the means with a 90% confidence interval, we also determined that the number of sparrows present in the control plot in 2004 was significantly less than in 2002 by almost 54%, or 1.5 sparrows per point. In 2005 the number of sparrows in the control plot returned to a level consistent with the 2002 survey. This indicates that there was an underlying environmental variable that drove sparrow densities downward during the course of our study, but was alleviated in the following year. This also demonstrates the usefulness of a BACI study design in teasing out the causes of observed variation. Our study design

accounts for this non-fire effect when assessing the extent and timing of recovery for the sparrow population in the burned plot.

The results of our MANOVA on sparrow counts indicate no significant effect of year alone, but a significant effect of the interaction between year and fire (Wilk's  $\lambda = 0.1638$ ,  $F = 4.90$ ,  $df = 6, 20$ ,  $P = 0.0031$ ). This suggests that sparrow density, in either the burned or control plot, is changing over time. The comparison of least squares indicates that in 2002 the burned and control plots were significantly different ( $P = 0.0029$ ), as would be expected given the virtual exclusion of sparrows from the burned plot in the first year post fire. A similar pattern was evident in 2003 ( $P = 0.0191$ ), with an additional difference between the points located entirely in the burned plot and those classified as edge ( $P = 0.05$ ). Again, sparrows were still absent from the burned habitat, which explains the observed differences between the burned and unburned plots. In 2004 and 2005 however, we saw no statistically significant differences between burned and unburned plots, indicating that by 2004 the burned plot had reached a density indistinguishable from the control.

### *Dispersal*

None of the 35 individuals caught and color banded in the burned plot prior to the fire has been seen again since the fire. The fate of these individuals is unknown although we do know they did not move to nearby adjacent unburned habitat as we did not find them in our control plot. The birds we have documented colonizing the burned plot have come from both within and outside the study plot. In 2004, five adults (four males and one female) that previously occupied the unburned plot in 2003 established territories in the burned plot, representing 26% of the total 2004 breeding population in the burned plot. Also, three birds

banded as nestlings in the unburned plot during the 2003 season established territories in the burned plot in 2004. In 2005 three adults (two males and one female) that previously occupied the unburned plot in 2004 established territories in the burned plot, representing 18% of the total 2005 breeding population in the burned plot. Of the forty-three birds banded as nestlings in 2004, three returned to their respective plots, and one that had been banded in the unburned plot established its territory within the burned plot. Also in 2005, three pairs of sparrows alternated nesting sites between the burned and unburned plots throughout the breeding season.

### *Nesting Success*

Between 2002 and 2005 we found and monitored 160 nests, 113 in the unburned plot and 47 in the burned plot. Our analysis of those nests monitored before the fire, in both the unburned and burned plot, indicate that the locations were statistically indistinguishable (Figure 3). The overall daily nest survival probabilities within the control plot remained relatively constant over the three years post-fire; the exception being a drop from 36% prior to the fire, to 14% in 2002 (Figure 3). The 2002 breeding season was a high water year and we know that peaks in water flows led to sharp drops in nest success (Baiser and Lockwood 2006). Sparrows began breeding in the burned plot in 2004. The 2004 and 2005 daily probabilities of nest survival for nests placed in burned habitat are indistinguishable from those placed in unburned habitat.

### *Vegetation Composition and Structure*

Vegetation composition is clearly influenced by fire, but shows signs of significant recovery two years after the fire (Figure 4). The global  $R$ -value for the ANOSIM was 0.142, which indicates that there is some degree of separation between years or treatment. Accordingly, none of the random permutations of the data yielded a global  $R$ -value larger than the observed, thus indicating that the sites show statistically different compositions ( $P = 0.001$ ). Pairwise comparisons between transects at each time interval since the fire illustrate where this difference arises (Table 3). Sample quadrats within the burn transect show a difference in composition between the year of the fire (B0) and the first and third year post-fire (B1 and B3). This indicates that the fire substantially altered species composition immediately post-burn. However, since the first year after the fire, composition has not changed. The lowest recorded  $R$ -value for comparisons between the burned and control transects occurs when the samples are compared two-years post burn ( $R = 0.083$ ). This  $R$ -value falls within the range of those obtained for comparisons across years but within the control transect.

According to the resulting eigenvalue loadings, the first Principal Component (PC1) represents a measure of vegetation height, specifically that of *Cladium jamaicense*, and the second Principal Component (PC2) represents a measure of overall vegetation cover and the amount of exposed bare ground (Table 4). Figure 5 illustrates that the fire substantially decreased overall vegetation height, removed sawgrass seedheads, and exposed more bare ground. The MANOVA results for PC1 indicated a significant effect of year since burn (Wilk's  $\lambda = 0.274$ ,  $F = 15.9$ ,  $df = 3, 18$ ,  $P = <0.0001$ ), and the interaction between year and treatment (Wilk's  $\lambda = 0.392$ ,  $F = 9.32$ ,  $df = 3, 18$ ,  $P = 0.0006$ ). The comparison of least square means indicated a significant difference the first month after fire ( $P = <0.0001$ ) as well as the



first year after fire ( $P = 0.023$ ) but no difference in subsequent years. Thus we see evidence of vegetation recovery in each successive year; however not until the third year do we see recovery to the extent that the number and height of sawgrass seedheads becomes indistinguishable between the burned and control plots. The results for PC2 similarly indicated a significant effect of year since burn (Wilk's  $\lambda = 0.383$ ,  $F = 9.68$ ,  $df = 3,18$ ,  $P = 0.0005$ ), and the interaction between year and treatment (Wilk's  $\lambda = 0.532$ ,  $F = 5.28$ ,  $df = 3,18$ ,  $P = 0.0087$ ). The comparison of least square means for PC2 indicated a significant difference only in the first month after fire ( $P = <0.0001$ ) but not afterward. Over the succeeding two years post-fire, the increased accumulation of both live and dead biomass shifted toward values typical for the control transect, regardless of year measured.

## DISCUSSION

Our study is unique in that the Cape Sable seaside sparrow is dependent on sub-tropical wet grasslands that are typical of the Everglades ecosystem but are rare worldwide. It has often been assumed that these wet grasslands behave as do temperate and Mediterranean grasslands in that they will suffer woody plant encroachment in the absence of fire (Beckage et al. 2003; Egler 1952). Based on this idea, it has been postulated that the Cape Sable seaside sparrow requires fire to persist in this landscape as its habitat will quickly succeed into an unsuitable state without fire (Taylor 1983; Werner 1975). We directly tested the latter assumption, and in the process we shed new light on the applicability of grassland management paradigms to the marl prairies of the Florida Everglades and similar wet grasslands (e.g., Pantanal).

Individual sparrows are apparently driven far from burned habitat, or perish due to the fire. Certainly any nests that are active at the time of a fire are lost, as are most recent fledglings, given that they are relatively weak flyers (Werner 1975). Sparrow habitat that has burned will remain unsuitable for sparrow breeding for at least two years after the fire largely because the vegetation structure necessary for sparrow breeding does not recover for two years. However, unburned habitat, even if it directly abuts burned spaces, will support sparrow densities and nesting success indicative of unburned habitat. When the burned habitat does recover it is very similar in species composition and vegetation structure to unburned places and the habitat shows no signs of being ‘enhanced’ based on our observation that sparrows re-occupy burned areas at densities indistinguishable from unburned areas. Recolonizing individuals will experience nest success probabilities that are indistinguishable from unburned habitat and equivalent to pre-fire habitat. The individuals that recolonize the burned site likely come from nearby habitat, and these individuals may be relocating breeding adults or first-year breeders. There is no evidence from this study that dispersal distances are so limited that a spatial pattern of time to recovery is apparent. However, this result may be restricted to fires that burn relatively small areas of sparrow habitat or to situations where a source population is within a few kilometers of the fire-affected places (we further consider these spatial effects below).

These results strongly support our scenario B, in which sparrow demography is immediately reduced after the fire, remains low for only a few breeding seasons following the fire, and returns to a level indistinguishable from unburned areas relatively quickly. This conclusion contradicts past studies and the prevailing wisdom that suggested Scenario A as the guiding model of Everglades marl prairie management for Cape Sable seaside sparrow

recovery (Taylor 1983; Werner 1975). The notion that Cape Sable seaside sparrows do not require fire for their long-term persistence and that marl prairie grasslands do not readily succeed to an unsuitable state for sparrows, or are not ‘enhanced’ by fire, is supported by noting that sparrow density in our control plot remained relatively stable over the course of this study. The control plot has not been burned since 1994, which is over 11 years of fire-free time. We did observe a slight, but significant, reduction in sparrow density in the control plot over the span of our study, but the fire-impacted population came back to this value, not the pre-burn values. This indicates that this decline was not due to the lack of fire, but rather to an unaccounted for environmental variable (e.g. food supplies, water levels).

These findings have several implications concerning the role of fire in Cape Sable seaside sparrow recovery efforts. Over the past twenty-five years the Cape Sable seaside sparrow has been reduced from 6,600 individuals (1981) to less than 2,500 individuals (2002) (Pimm et al. 2002). One of the sparrow subpopulations is feared to be extirpated, and two others are at such low densities that they are considered near extirpation (Pimm et al. 2002). In our study, which takes place in the center of one of the densest subpopulations, fire has removed sparrows from the burned area for two years. It is not clear how such an impact to an already small population affects longer-term persistence of the subspecies. However, it clearly cannot help. The degree of harm caused by the Lopez fire was likely ameliorated by the fire’s relatively small spatial extent, and by the fact that there was occupied sparrow habitat surrounding the fire scar. In cases where the fire is large, or it occurs within a subpopulation that is near extirpation, greater harm will occur. Furthermore, the Lopez fire was a typical early wet season fire in the sense that plant mortality was restricted to primarily above-ground components of the vegetation. The intensity and seasonality of fire will have a

profound effect on the regeneration of suitable sparrow habitat. For example, a hot, dry fire which consumes all above-ground and below-ground vegetation may result in a longer return interval with unpredictable species composition. This same scenario followed by a high-water period has resulted in the conversion of marl prairie to marsh vegetation which may or may not revert to marl prairie depending on site hydrology (Pimm et al. 2002).

Our results argue for careful consideration by Everglades fire management of population size and fire extent when managing fire within occupied sparrow habitat. In cases where fuel reduction is necessary for reasons other than the protection of the sparrow, a fire management plan which allows frequent, large fires to burn sparrow habitat will undoubtedly have a negative impact on the species. Instead, a plan which maximizes the time between large fires to at least 10 years, and then restricts all fires from burning within very small subpopulations, will have the best chance of providing refuge to displaced sparrows, as well as reduce the risk of a single fire event driving a subpopulation to extirpation. What is now needed is a landscape-level understanding of both fire and the interplay between hydrology and fire. If a landscape-level occupancy analysis supports our results on the plot-level scale, we will feel much more confident in setting a particular fire frequency to best manage the sparrow while still meeting the needs of the greater Everglades ecosystem.

Our findings lend considerable credence to the idea that more empirical studies must be completed to elucidate the effect of disturbance on the demography of endangered species. To assume that because an organism resides in a disturbance-prone ecosystem it therefore must benefit from such events, is to oversimplify the relationship and could very well lead to mis-management. Instead, by understanding the impact that disturbance has on species of particular concern, we can better decide when and where to allow disturbances to occur in

order to maximize benefits to all members of the ecosystem. We do not see the management for the sparrow as conflicting with the management of other species of concern or the Everglades ecosystem as a whole. In fact, the sensitivity of the species to both hydrological patterns (Curnutt et al. 2000; Curnutt et al. 1998; Lockwood et al. 1997) and fire suggests to us that the species may be acting as a ‘canary in the coalmine’ for the multi-billion dollar restoration plan currently in progress.

## LITERATURE CITED

- Aebischer, N., 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* 46.
- Askins, R., 2002. *Restoring North America's Birds: Lessons from Landscape Ecology*. Yale University Press.
- Baiser, B.H., Lockwood, J.L., 2006. The influence of water level on breeding success of Cape Sable seaside sparrows (*Ammodramus maritimus mirabilis*) : Getting the water right for the recovery of an endangered species in the Everglades. In Prep.
- Beckage, B., Platt, W.J., Slocum, M.G., Pank, B., 2003. Influence of the El Nino Southern Oscillation on fire regimes in the Florida everglades. *Ecology* 84, 3124-3130.
- Brawn, J., Robinson, S., Thompson III, F., 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32, 251-276.
- Clarke, K., Warwick, R., 1994. *Change in marine communities: an approach to statistical analysis and interpretation*. Natural Environment Research Council.
- Curnutt, J.L., Comiskey, J., Nott, M.P., Gross, L.J., 2000. Landscape-based spatially explicit species index models for Everglades restoration. *Ecological Applications* 10, 1849-1860.
- Curnutt, J.L., Mayer, A.L., Brooks, T.M., Manne, L., Bass, O.L., Jr., Fleming, D.M., Nott, M.P., Pimm, S.L., 1998. Population dynamics of the endangered Cape Sable seaside-sparrow. *Animal Conservation* 1, 11-21.
- DeAngelis, D.L., White, P.S., 1994. Ecosystems as Products of Spatially and Temporally Varying Driving Forces, Ecological Processes, and Landscapes: A Theoretical Perspective, In *Everglades: the ecosystem and its restoration*. eds S.M. Davis, J.C. Ogden, pp. 9 - 28. St. Lucie Press, Delray Beach, FL.

- Egler, F., 1952. Southeast saline Everglades vegetation, Florida and its management. *Plant Ecology* 3, 213-265.
- ESRI, 2005. ArcGIS 9.0. Environmental Systems Research Institute, Redlands, CA.
- Gunderson, L.H., Snyder, J.R., 1994. Fire patterns in the southern Everglades, In *Everglades: the ecosystem and its restoration*. eds S.M. Davis, J.C. Ogden, pp. 291-306. St. Lucie Press, Delray Beach, FL.
- Hazler, K., 2004. Mayfield Logistic Regression: A practical approach for analysis of nest survival. *The Auk* 121.
- Jakalaniemi, A., Tuomi, J., Sikamkaki, P., 2006. Conservation of species in dynamic landscapes: Divergent fates of *Silene tatarica* populations in riparian habitats. *Conservation Biology* 20, 844-852.
- Law, B., Dickman, C., 1998. The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodiversity and Conservation* 7, 323-333.
- Lockwood, J.L., Fenn, K.H., Caudill, J.M., Okines, D., Bass, O.L., Duncan, J.R., Pimm, S.L., 2001. The implications of Cape Sable seaside sparrow demography for Everglades restoration. *Animal Conservation* 4, 275-281.
- Lockwood, J.L., Fenn, K.H., Curnutt, J.L., Rosenthal, D., Balent, K.L., Mayer, A.L., 1997. Life history of the endangered Cape Sable seaside sparrow. *Wilson Bulletin* 109, 720-731.
- Lockwood, J.L., Ross, M.S., Sah, J.P., 2003. Smoke on the water: the interplay of fire and water flow on Everglades restoration. *Frontiers in Ecology and the Environment* 1, 462-468.
- Madden, E.M., Hansen, A.J., Murphy, R.K., 1999. Influence of prescribed fire history on habitat and abundance of passerine birds in northern mixed-grass prairie. *Canadian Field-Naturalist* 113, 627-640.

- Manly, B.F.J., 2001. Statistics for Environmental Science and Management. Chapman & Hall.
- Mayfield, H., 1975. Suggestions for calculating nest success. Wilson Bulletin 87, 456-466.
- Moran-lopez, R., Sanchez, J.M., Costillo, E., Corbacho, C., Villegas, A., 2006. Spatial variation in anthropic and natural factors regulating the breeding success of the cinereous vulture (*Aegypius monachus*) in the SW Iberian Peninsula. Biological Conservation 130, 169-182.
- Pickett, S.T.A., White, P.S. eds., 1986. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego, CA.
- Pimm, S.L., Lockwood, J.L., Jenkins, C.N., Curnutt, J.L., Nott, M.P., Powell, R.D., Oron L. Bass, J., 2002. Sparrow in the grass: a report on the first ten years of research on the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). Report to the National Park Service. Everglades National Park, FL.
- Reyment, R.A., Blackith, R.E., Campbell, N.A., 1984. Multivariate Morphometrics. Academic Press, Inc., London.
- Sousa, W.P., 1984. The Role of Disturbance in Natural Communities. Annual Review of Ecology and Systematics 15, 353-391.
- Taylor, D.L., 1983. Fire Management and the Cape Sable Sparrow, In The Seaside Sparrow: Its Biology and Management. eds T.L. Quay, F.J.B. Jr., D. Lee, E.F. Potter, C.S. Robbins, pp. 147 - 152. North Carolina Biological Survey and North Carolina State Museum, North Carolina.
- Tucker, J.W., Robinson, W.D., Grand, J.B., 2006. Breeding productivity of Bachman's sparrows in fire-managed longleaf pine forests. Wilson Journal of Ornithology 118, 131-137.
- Werner, H., 1975. The Biology of the Cape Sable seaside sparrow, In Report to US Fish and Wildlife Service. Everglades National Park, Homestead.



Whelan, R.J., Birks, H.J.B., Wiens, J.A., 1995. The Ecology of Fire. Cambridge University Press, Cambridge.

The data analysis for this paper was generated using SAS software, Version 9.1, of the SAS System for Windows. Copyright © 2002 – 2003, and StatView software, Version 5.0. Copyright © 1992 – 1998, SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA.

## LIST OF TABLES

Table 1. Mean values ( $\pm$ SD) of the total number Cape Sable seaside sparrows detected at point count locations, Everglades National Park, 2002-2005. Sparrow density was lower for two years following fire in the burned area, returning in the third year to a level consistent with the unburned area.

Treatment	n	2002 Average	2003 Average	2004 Average	2005 Average
<b>Burned</b>	4	0.72(0.40)	0.65(0.47)	1.44(0.77)	2.06(1.41)
<b>Edge</b>	3	1.79(1.01)	2.17(0.88)	1.29(0.52)	2.13(0.38)
<b>Unburned</b>	8	3.03(0.97)	2.09(0.74)	1.63(0.80)	2.38(0.98)

Table 2. Overall nest survival probabilities for Cape Sable seaside sparrows based on daily survival estimates and calculated using the Logistic Mayfield Method (Hazler 2004). The overall nest survival probability represents the probability that a single nest will survive from the beginning of egg-laying until the fledging of the last nestling. The value is derived by raising the daily nest survival probability to the average number of days in the nesting cycle. In the case of the CSSS, there are 12 egg days, up to 4 hatching days, and 9 nestling days for a total of 25 days. The overall nest survival probability in the unburned area remains relatively consistent over the study. In 2002 we witnessed a decrease in nest survival, most likely due to a water pumping station which went into operation during the breeding season. After two seasons of exclusion from the burned plot, the 2004 and 2005 survival probabilities for those birds that recolonized the area was indistinguishable from pre-fire levels.

<i>Nest Survival Probability for CSSS</i>					
	<i>Pre Fire</i>	<b>2002</b>	<b>2003</b>	<b>2004</b>	<b>2005</b>
<b>Burned</b>	0.414 (n=7)	no nests-(0)	no nests (0)	0.407 (n = 14)	0.265 (n = 25)
<b>Unburned</b>	0.364 (n=14)	0.137 (n = 25)	0.325 (n = 29)	0.313 (n = 26)	0.461 (n = 41)

**Table 3.** Pairwise Analysis of Similarity (ANOSIM) results for vegetation species composition (live only) between burned (B) and unburned (U) transects, one-month (0), one-year (1), two-years (2), and three-years (3) post fire. Results are from Mote Carlo simulation of 10000 permutations.

		Comparison	Observed <i>R</i> - value
Control Transect Through Years		U0,U1	0.103
		U0,U2	0.079
		U0,U3	0.054
		U1,U2	0
		U1,U3	0.038
		U2,U3	0.002
Burned Transect Through Years		B0,B1	<b>0.17</b>
		B0,B2	0.092
		B0,B3	<b>0.217</b>
		B1,B2	0.058
		B1,B3	0.064
		B2,B3	0.044
Burned to Unburned Through Years	<b>B0</b>	B0,U0	<b>0.311</b>
		B0,U1	<b>0.273</b>
		B0,U2	<b>0.188</b>
		B0,U3	<b>0.305</b>
	<b>B1</b>	B1,U0	<b>0.314</b>
		B1,U1	<b>0.182</b>
		B1,U2	<b>0.206</b>
		B1,U3	<b>0.156</b>
	<b>B2</b>	B2,U0	<b>0.138</b>
		B2,U1	<b>0.117</b>
		B2,U2	0.083
		B2,U3	<b>0.13</b>
	<b>B3</b>	B3,U0	<b>0.154</b>
		B3,U1	<b>0.229</b>
		B3,U2	<b>0.169</b>
		B3,U3	0.102

**Table 4.** Eigenvector loadings for Principal Component Analysis. Values above 0.35 were deemed important and used in describing each Principal Component axes. Principal Component 1 (PC1) represents a measure of *Cladium jamaicense* seedhead height and seedhead density. Principal Component 2 (PC2) represents the amount of exposed bare ground, and amount of standing dead cover.

<b>Variable</b>	<b>PC 1</b>	<b>PC 2</b>
Max height of <i>Cladium jamaicense</i> Seedheads	<b>-0.429</b>	-0.33
Max height of vegetation	<b>-0.393</b>	0.061
Is max height <i>C. jamaicense</i> seedhead? N=0, Y=1	<b>-0.384</b>	<b>-0.378</b>
Density of seedheads / plot	<b>-0.381</b>	<b>-0.362</b>
Dead cover	-0.311	<b>0.353</b>
Effective height (cm)	-0.306	0.217
Soil depth (max)	-0.055	0.273
Soil depth (min)	0.022	0.307
Live:dead biomass	0.289	-0.313
Bare ground	0.302	<b>-0.418</b>

## FIGURE LEGENDS

**Figure 1.** Map showing South Florida coastline with Everglades National Park boundary. Crosshatched areas represent extent of Cape Sable seaside sparrow habitat. The Lopez fire (solid black) is shown originating from the eastern boundary of the park, and extending westward, bisecting a subpopulation of the sparrows. Inset: Detail of the Lopez fire (solid black) and our 2 km x 1 km study plot (hatched rectangle).

**Figure 2.** Three theoretical scenarios of the effect of fire on *A. m. mirabilis*. The horizontal dashed line represents the control plot, where no change is occurring. After fire, each scenario is predicted to show a drop in a measured parameter, which in our case would be either sparrow density or nesting success. This condition is expected to continue for some period of time, at which point the burned habitat will show either a measurable degradation due to fire (C), no effect of fire (B), or enhancement by fire (A). Our time scale is based on previous research by Pimm et al. (2001), and work by Werner (1975) and Taylor (1983).

**Figure 3.** The daily probability of survival for nests of *A. m. mirabilis* calculated for each year in both the unburned area (solid line with open squares) and burned plot (dashed line with solid triangles) ( $\mu \pm 95\%$  CI).

**Figure 4.** Non-metric Multi Dimensional Scaling (NMDS) ordination for *A. m. mirabilis* habitat composition. Each symbol represents a single plot. Data is divided by treatment and time since fire; one month (triangles), one year (inverted triangles), two years (circles) and three years (squares). Open symbols represent vegetation plots in the burned treatment (n =

22) and solid symbols representing those in the control (n=22). This ordination indicates very little compositional difference between treatments and time-since fire, supporting the idea that composition recovers quickly following fire.

**Figure 5.** Principal Component Analysis (PCA) for *A. m. mirabilis* habitat structure.

As above, each symbol represents a single plot. Data is divided by treatment and time since fire; one month (triangles), one year (inverted triangles), two years (circles) and three years (squares). Open symbols represent vegetation plots in the burned treatment (n = 22) and solid symbols representing those in the control (n=22). Segregation is evident after the first month post fire, characterized by shorter vegetation, fewer *Cladium jamaicense* seedheads, more bare ground, and less dead cover. In each successive time period, the burned plots increase convergence toward the control, but are noticeably slower on the PC1 axis than on the PC2, as bare ground is recovered sooner than vegetation height.

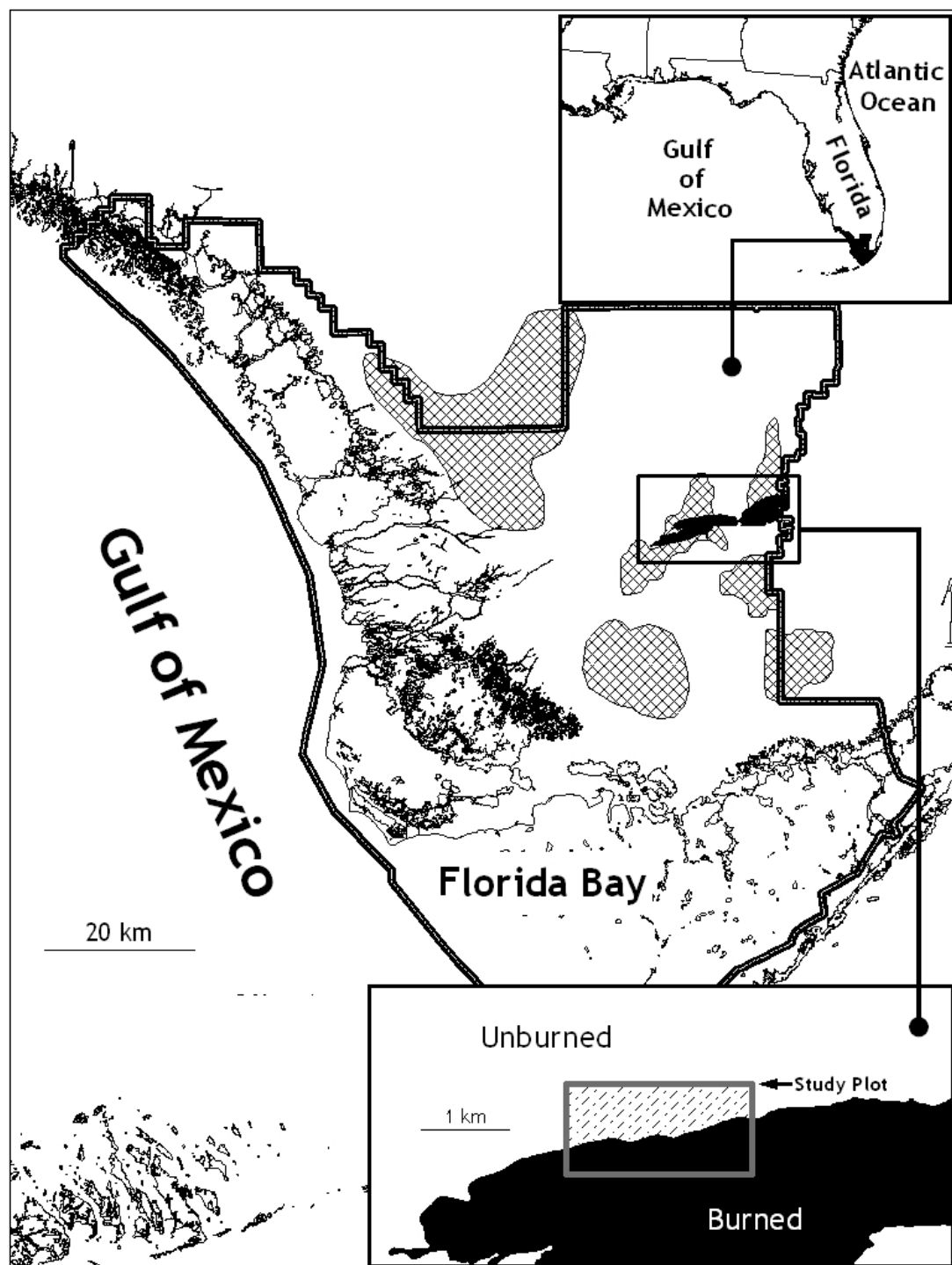


FIG. 1.



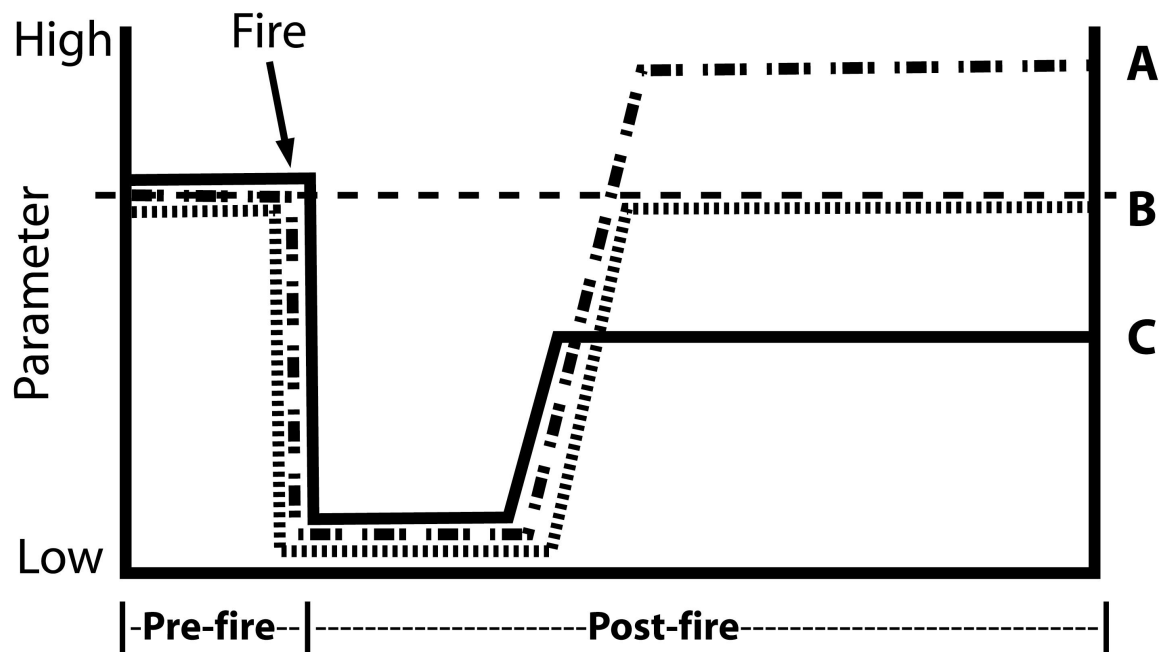


FIG. 2.

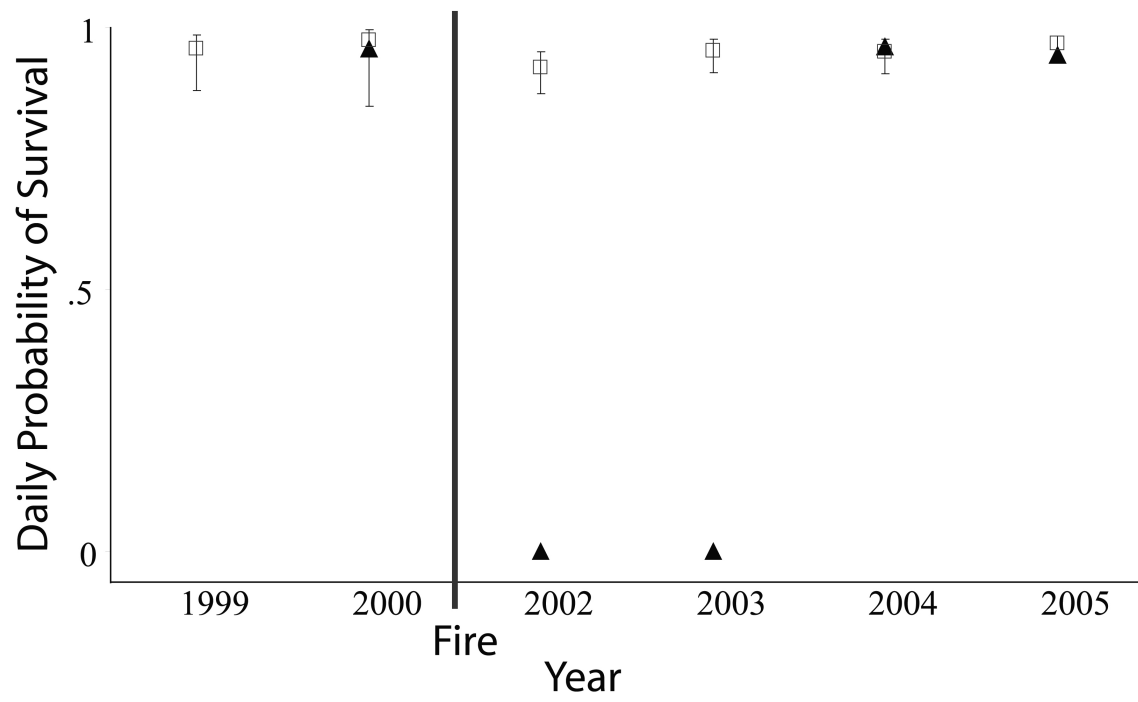


FIG. 3.

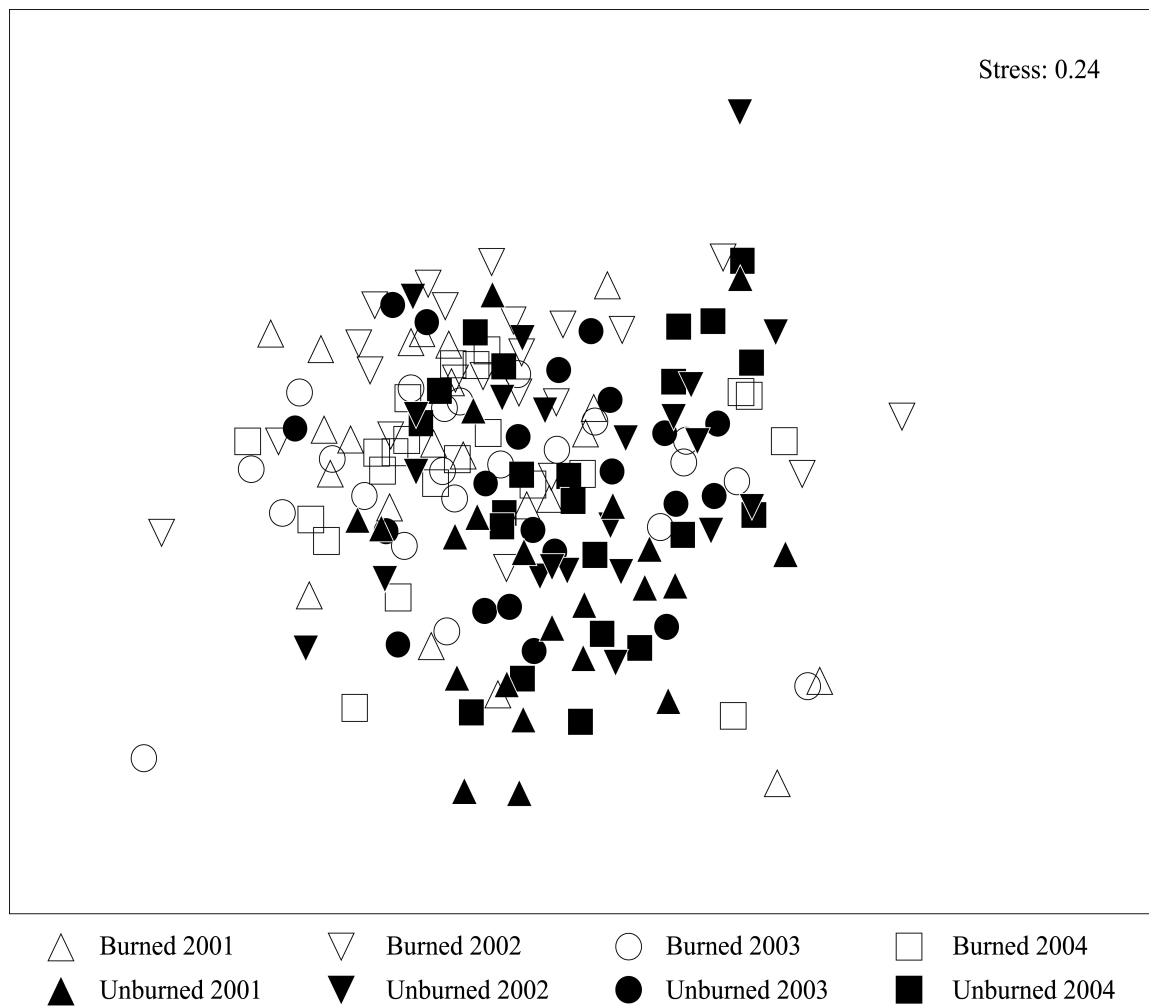


FIG. 4.

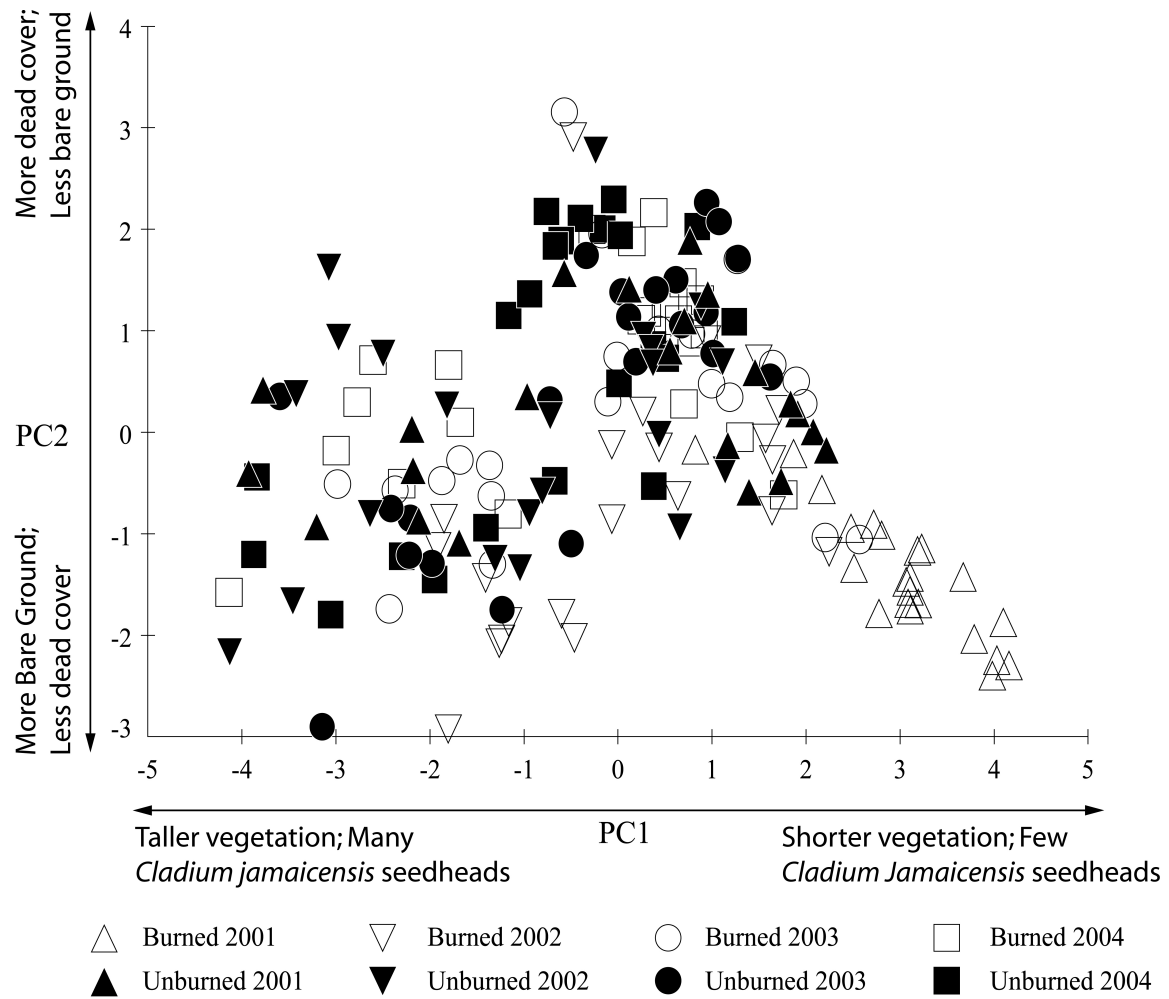


FIG. 5.

## Chapter 2

# **IMPORTANCE OF FIRE FOR CHANGES IN CAPE SABLE SEASIDE SPARROW SITE OCCUPANCY IN EVERGLADES NATIONAL PARK, FLORIDA**

David A La Puma • Phillip Cassey • Julie L. Lockwood

David A. La Puma (Corresponding Author) • Julie L. Lockwood

Department of Ecology, Evolution & Natural Resources

Rutgers University, 14 College Farm Road

New Brunswick, New Jersey, 08901

E-mail: [lapuma@eden.rutgers.edu](mailto:lapuma@eden.rutgers.edu)

Phone: 732 932 3313 / Fax: 732 932 8746

Phillip Cassey

Centre for Ornithology, School of Biosciences

Edgbaston B15 2TT

University of Birmingham, United Kingdom

## ABSTRACT

Understanding how disturbance regimes affect population dynamics is critical for effective species conservation. We determined whether the changes in population occupancy of Cape Sable Seaside Sparrows (*Ammodramus maritimus mirabilis*) were reflected in the landscape level patterns of fire within the Everglades ecosystem. We characterized fire within sparrow habitat using a 16-year fire history geodatabase. We then tested whether sparrow site usage differed between burned versus unburned sites, and considered whether fire size, cause of ignition, or seasonality, as well as soil depth around each survey point, determined the probability of site occupancy by sparrows in the first year post-fire. Finally, for those points that burned, we looked for a pattern between sparrow occupancy and the time since fire. Our results demonstrate that the fire history of currently occupied sparrow habitat is consistent with patterns previously reported for the greater Everglades ecosystem. Sparrows occupy recently burned sites at a significantly lower probability than they occupy points which have not burned in five or more years. None of the fire characteristic variables we considered had a significant influence on probability of sparrow site usage during the two years post-fire. For those points that burned, sparrow occupancy follows a quadratic relationship increasing up to 11 years post-fire and then decreasing thereafter. We suggest that while fire is a natural component of the Everglades ecosystem and sparrows show an ability to recover from fires, the spatial configuration of the remaining sparrow populations requires that they be protected from fire until a substantial recovery is achieved.

**Key Words:** *Ammodramus maritimus mirabilis*, Avian Conservation, Fire, Florida Everglades, Occupancy.

## INTRODUCTION

Natural disturbances are important elements of landscape dynamics that can spatially structure the distribution and abundance of populations and species (e.g., meta-population or source-sink dynamics) (Hastings 2003). As well as directly perturbing key habitat, disturbance may have profound effects on factors regulating populations, such as prey availability, release or introduction of predators or competitors, or the creation or destruction of refugia (Levin and Paine 1974; Pickett and White 1986; Sousa 1984). The effect of disturbance is predicated on the exposure of the species to such events over evolutionary time. There are many examples of disturbance regimes being introduced or altered such that the species affected are unable to adjust (Brawn et al. 2001; Hunter et al. 2001; Martin et al. 2006). In the most extreme cases, the introduction or alteration of disturbance may drive a species to extinction (Lande 1993).

The Everglades of south Florida is a fire-prone ecosystem (Beckage et al. 2005; Gunderson and Snyder 1994; Platt et al. 2002) that harbors many fire dependent native species and provides refuge to 31 species federally listed as Threatened and Endangered. Recent and extensive urbanization of the ecosystem has altered the fire regime of the remaining natural areas (Lockwood et al. 2003b), while effects of this altered fire regime on these species remains largely unknown. Here we explore the landscape dynamics of fire on the range-wide site occupancy of one such species, the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*).

The Cape Sable Seaside Sparrow is endemic to the Everglades ecosystem and, like many other species in south Florida, has lost critical habitat to development. However, the main threats frequently hypothesized to affect sparrow numbers and geographic extent are alterations of water flows (Curnutt et al. 1998; Jenkins et al. 2003; Nott et al. 1998) and fire regimes (La Puma et al. 2007; Pimm et al. 2002). Currently the total estimated number of sparrows stands at less than 3200 individuals, distributed among six populations within or adjacent to Everglades National Park (A–F) with B and E constituting over 95% of all remaining individuals (Fig. 1). Recovery of the sparrow is intimately tied to the multi-billion dollar restoration of Everglades water flows now underway (Walters et al. 2000). In particular, there is the expectation that returning water flows to a more natural state will simultaneously restore all associated ecosystem processes including fire regimes (Lockwood et al. 2003a). However, the relationship between water flows, fire, and sparrow population dynamics is made complex because of multiple feedback loops between these landscape processes and the plant communities that support suitable sparrow habitat (Lockwood et al. 2003a).

From 2001 to 2005, La Puma et al. (2007) assessed the local response of Cape Sable Seaside Sparrows to a single fire event in Everglades National Park (ENP). Results from this single sparrow population (E; Fig. 1) showed that vegetation structure and composition returned to pre-burn conditions between one and two years following fire. However no sparrows used the recovering habitat during the two breeding seasons following the fire, and no sparrows that were banded in the burned area prior to the fire had been re-sighted since, despite major efforts to find them. Nevertheless, sparrows returned in the third year post-fire at densities and with rates of nesting success statistically indistinguishable from the unburned



adjacent habitat and have remained as such ever since. These results led to the conclusion that fire had an immediate negative effect on sparrow habitat usage, however, the fire did not appear to have any lasting positive, or negative, effects on the ability of this greater population to recolonize or reproduce (La Puma et al. 2007).

Despite the advances this study made in our understanding of the response of Cape Sable Seaside Sparrows to fire, extrapolating larger ecological and management inferences are problematic as it is quite possible that sparrows and their habitat do not react to fire in the same manner across the entirety of their current range. For example, slight differences in soil depth or seasonal water flow could influence the rate at which suitable breeding habitat returns following a fire (Ross et al. 2007; Taylor 1983). Similarly, the fire studied by La Puma et al. (2007) was an early dry-season fire that produced relatively high temperatures and left little in the way of unburned vegetation mosaic. Fires that burn at other times of the year may have very different impacts on sparrow return times due to fire extent and configuration. Finally, the spatial structure of the sparrow population may have an influence on the rate of return after a fire, such that isolated populations will not recover as quickly as those that are as close to a source population.

Here we test the effect of site-specific variables and document the relationship between sparrow site occupancy and fire in the Everglades. To do this we combine a fire geodatabase spanning 16 years (1989-2005) with 13 years of sparrow range-wide occupancy information (1992-2005). We characterize the fire regime within sparrow habitat across the 16-year span of the geodatabase to assess whether the area of each sparrow population has burned more frequently and to greater extent relative to the others, and whether fire regimes in sparrow habitat are qualitatively different from regimes experienced by the ecosystem as a

whole. Among the different sparrow populations, we compare sparrow site occupancy between burned and unburned sites. We also evaluate the role of fires of different extent, season, and type to test whether characteristics of the fires themselves significantly influence the probability that sparrows will occupy a site one and two years post-fire. We also test for a relationship between soil depth and the time required for sparrows to return after a fire event. Finally, we calculate the time-since-fire for each survey year and then estimate how fire events directly affect sparrow site occupancy across a 13-year period.

## **METHODS**

### *Fire Characterization*

We utilized a fire history geodatabase maintained by Everglades National Park (ENP) Fire Management that consists of perimeters of all fires recorded within ENP from 1989 – 2005. Fire Management personnel map the perimeter of all fires soon after the fire is discovered or set (as managed prescribed burns). Although variable through time, the primary means of mapping fires since 1990 has been to fly around the perimeter of a fire in either a fixed-winged aircraft or helicopter and map the edge using a Global Positioning System (GPS). In some cases the perimeter was mapped by walking the edge with a GPS unit. Prior to 1990, fire perimeters were hand-drawn on topographic maps and later digitized into a Geographic Information System (GIS). Given this variability in perimeter estimation methods, we cross-validated all fires using the hard-copy records maintained by ENP.

Using ArcGIS 9.2 we selected all fires that intersected the six Cape Sable Seaside Sparrow population boundaries (see below for boundary definitions) and derived the following variables for each fire: season (wet or dry), ignition source (human, lightning,

prescription), as well as the spatial extent of the fire. Because the Everglades are sub-tropical, they experience distinct wet and dry seasons. Fire regimes can be strongly structured by such a climatic pattern for a variety of reasons (Beckage et al. 2003; Slocum et al. 2007). For our analyses, we wanted to derive a wet season start date that reflected the increase in average water depths within sparrow habitat. We posited that higher water levels associated with the wet season would limit the extent of any fire that was ignited at this time. Thus, we needed to derive wet season start date that was based on water depths within sparrow habitat and was not exclusively reflective of the meteorological definition of the wet season. To do this we used the steepest 3-day average increase in water levels, after which the water levels did not drop below the initial depth. We used three hydrological stations located within sparrow populations to determine our wet-season onset date.

Once the wet season onset dates for each year were derived, fires were categorized as either ‘wet’ or ‘dry’ according to the date the fire was discovered. In most years drying down occurred at the end of the calendar year, and so we only used our onset of wet season date as the breaking point for all fires within each year. However, in a few years wet conditions were temporary and water levels within sparrow habitat dried down in late November or early December. In those years we applied a similar 3-day average water depth decrease criterion to determine the onset of the dry conditions, and classified fires accordingly.

To determine the ignition source of each fire, we used the ‘fire type’ and ‘cause’ attributes within the ENP fire geodatabase. These data provide specific causes of each fire, along with information on the course of action taken by Everglades Fire Management. We

used this information to assign each fire to one of three groups; human-ignited or incendiary, natural or lightning-ignited, or management-ignited prescription burns.

To derive the size of each fire, we used the sizes reported in the fire geodatabase attributes table. However, in several cases this data was missing, and thus for these fires we used ArcGIS 9.2 to calculate the size of the fire using the fire perimeter polygon. We then calculated both the spatial extent of sparrow habitat burned (SEB) and the total area of sparrow habitat burned (TAB) for each population. SEB accounts for the spatial coverage of all fires over the period of record relative to the geographic extent of the population in which these fires occurred (see below for definition of population extent). This value will rarely reach 100% since small, unburned areas tend to persist in all populations, even when fires are frequent and large. The TAB accounts for the sum of all areas burned by fires, regardless of spatial orientation, such that the area of overlapping fire perimeters within and between years will be counted in a cumulative fashion. Therefore TAB may exceed 100% and in most cases is greater than SEB for the same population. Together these metrics describe the frequency and spatial arrangement of fires within sparrow habitat.

### *Estimating Sparrow Habitat Extent and Occupancy*

Kushlan and Bass (1983) established a range-wide survey protocol for estimating the spatial extent of Cape Sable Seaside Sparrow habitat and for estimating the sparrow's overall population size. This survey calls for observers to be dropped at points regularly spaced at 1km intervals across all suspected sparrow habitat. The observers then record all sparrows seen or heard within a seven-minute interval. This survey was originally conducted in 1981, and was repeated in its entirety in 1992. Since 1992, the same sites and protocol have been

repeated annually (Curnutt et al. 1998). During the 2001 survey period, four soil depth measurements were taken at each survey point location. We used the average of these four measurements to derive a soil depth variable for each survey location.

The sparrow range-wide survey, at a minimum, provides annual information on the spatial extent of occupied sparrow habitat (Cassey et al. 2007). We used the site occupancy information produced from the survey in two distinct ways. First, we determined the maximum overall extent of sparrow habitat in the Everglades post-1981. To do this we isolated the set of survey sites that detected at least one sparrow since 1981 and extracted these points from the set that have been annually surveyed but have never had sparrows recorded as present. Of the 844 sites that were originally surveyed in 1981, 169 (38%) never detected a sparrow and thus were excluded from further analyses. Of the remaining points, 427 were surveyed frequently enough since 1992 (at least six times) to be included in the following analyses. These points were divided into populations according to the definition provided by Curnutt et al. (1998), thus allowing us to calculate the spatial extent of each population.

These 427 survey points were overlain with the fire record for each year in the geodatabase (1989 thru 2005). When a survey point intersected with a fire perimeter polygon, the fire date was compared with the survey date to determine if the survey information was taken before or after the fire. If the survey information was taken after the fire, the point was labeled as 'burned' in that year, and given the attributes associated with that fire (e.g., extent, season, ignition source) and soil depth at the survey point (measured in 2001). For every

survey year following a known fire event we calculated the time since a survey point was burned (time-since-fire).

Second, we used the information from each range-wide sparrow survey to calculate annual estimates of the probability of site occupancy from 1992 to 2005. We followed the methods of Cassey et al. (2007) and considered sparrow occupancy ( $\psi$ ) as the fraction of survey sites within an area of interest where sparrow abundance is  $> 0$  (MacKenzie et al. 2002). Because we only consider sites where sparrows have been detected at least once since 1981, our estimates of sparrow occupancy cannot be compared with the rates of change in occupancy sensu Cassey et al. (2007). Instead here we are interested only in the response of sparrow occupancy to fire events. Thus we pool all survey information that was taken at sites that were classified as one-year-post-fire, two-years-post-fire and so on, and then calculate the proportion of survey sites in each time-since-fire group that were occupied.

We used a mixed model logistic regression to test a series of different models that estimate the slope of change in occupancy,  $\psi$ , through time. First, we tested whether occupancy differed between sites that burned one year previous versus sites that had not burned in at least five years. Second, we tested whether attributes of the fires themselves or the survey location (fire area, fire type, season, soil depth) could explain the variance in occupancy observed within sites that had burned one and two years previous. Finally, we considered time-since-fire as a continuous variable and looked for trends in occupancy across annual time-since-fire categories up to 13-years post-fire.

We initially calculated these trends in occupancy across the entire range of the subspecies (treating the six populations as random effects). We then compared this analysis with results obtained from calculating trends within populations that are currently small (A,

C, D, and F, estimated average site occupancy  $< 0.1$ ) and those that are large (B and E, estimated average site occupancy  $> 0.2$ , Cassey et al. 2007).

Each sparrow population has a unique trajectory of site occupancy (see Cassey et al. 2007), and survey sites are nested within both USGS orthophoto quadrangles (quads) and within populations. Because sites are not spatially independent in terms of environmental conditions (e.g., water flows, rainfall), we controlled for these nested ‘blocking’ elements as random effects in all our models. In particular, we evaluated if an estimated slope of change in  $\emptyset$  was less than 0 (significance level  $\alpha = 0.05$ ). Following Cassey et al. (2007) we included year as a continuous fixed effect in the point estimate models of sparrow occupancy. Linear models of the relationship between sparrow occupancy and time-since-fire were constructed with time-since-fire as both a continuous fixed effect, and a categorical fixed effect for ease of presentation (see Figs. 5 and 6). All analyses were conducted in SAS v 8.2.

## RESULTS

### *Fire History in Sparrow Habitat*

Of the 134 fires that burned sparrow survey points between 1989 and 2005, 23% were either accidental, or deliberately ignited with malicious intent (hereafter referred to as “human-ignited incendiary fires”), 33% were natural lightning strikes, and 44% were management-ignited prescribed burns. The largest single fire during this period was the Ingraham Fire, which burned from May to July of 1989, and burned a total of 36,339 hectares. This naturally ignited fire contributes > 40% of the total area burned during the study period. Among the remaining fires, human-ignited incendiary fires accounted for the greatest number of dry-season fires ( $n = 21$ ) and burned the majority of the total area during the dry season (16,142 hectares). Very few human-ignited incendiary fires occurred in the wet season ( $n = 9$ ) and averaged one-quarter the size of those that burned in the dry season. Natural fires, which are tied directly to thunderstorms during the wet season (Beckage et al. 2003; Slocum et al. 2007), accounted for 40% of all fires that together burned 5,149 hectares from 1989 – 2005. The average size of these lightning fires was 136 (std err = 218) hectares. Several smaller naturally ignited fires (excluding the 1989 Ingraham fire) occurred during the dry season, averaging 14 (std err = 14) hectares in size, with a maximum size of 33 hectares. Management-ignited fires accounted for the largest area burned during the wet season over the study period (27,895 hectares).

When considering sparrow population boundaries, the total area burned (TAB; the cumulative area burned over all years within each population) was considerably greater than the spatial extent burned (SEB; the spatial coverage of all fires within a population) for all populations except for A (Table 1). Both values for population A were nearly



indistinguishable (TAB= 3,371ha, SEB= 3,220ha), indicating that fires were small and non-overlapping in this part of the landscape. All five remaining populations had TAB values >100%, indicating that 6% or more of their total geographic extent burned per year, between 1989 and 2005.

### *Occupancy Trends*

Across years the number of survey points included in our analysis ranged from 349 (1999) to 160 (1994). Just over half (56%) of the survey points included in our analyses (of  $n = 427$  points) have not burned since 1989. Across populations the proportions of survey points burned at some time between 1989 and 2005 are significantly different (Chi-square test of homogenous proportions;  $X^2 = 89.8$ ,  $P < 0.001$ ; Fig. 2). The average percentage of burned survey points per population was 69% and ranged from 13% of population A to 95% of population E. Excluding population A the proportions are more homogenous but still significantly different (Chi-square test of homogenous proportions;  $X^2 = 16.7$ ,  $P = 0.002$ ). When we calculated the percentage of survey points burned in any given year, the proportion of points burned exceeded 5% in six out of the 16 years with the greatest proportion of survey sites burning in the 1989 Ingraham fire (29%).

Controlling for population, and quad (nested within population) as random effects and including year as a fixed effect, we examined the proportion of survey sites occupied by sparrows in the first survey following a fire event compared with sites that had not burned for at least five years (i.e. unburned habitat). We show that sparrows occupy survey sites at a significantly lower rate one-year post fire as compared to occupancy in unburned habitat (estimate  $\pm$  std err =  $0.78 \pm 0.25$ ,  $t = 3.05$ ,  $P = 0.002$ ; Fig. 3).

Although occupancy was significantly lower after a fire there was enough variability in sparrow occupancy that the average occupancy during the first survey was greater than zero (Fig. 3; 10% [std err = 4%]). It is therefore of interest to know whether this variability can be explained by any characteristics of the fires themselves. For all fire events, including year and controlling for nested population structure as random effects, we tested the influence of fire extent (Log10 hectares), fire type (human ignited, natural, management ignited), season (wet, dry), and soil depth at the survey point (meters) on site occupancy in the survey year immediately after a fire event. Following fire events, none of the four terms analyzed were associated with significant trends in site occupancy (Table 2).

When we track occupancy trends beyond the first year post-fire we see that, following a fire event, average sparrow occupancy initially increases as the number of years without a fire increases (Fig. 3). Controlling for year, population, and quad (nested within population) the change in sparrow occupancy with time-since-fire across a period of 17 (1989 – 2005) years is best modeled by a quadratic relationship (Fig. 3).

Because of the different frequencies of fire events (Fig. 2) and trends in site occupancy (Cassey et al. 2007) between populations, it may be unlikely that this average model is a good description of the relationship between time-since-fire and sparrow occupancy for each of the individual populations. Separately, occupancy in the small populations (excluding A; see discussion) and the large populations are, on average, best modeled by quadratic equations with time-since-fire (Fig. 4). In populations B, C, and E the site occupancy of recently burned points (1-2 survey years after fire) is significantly lower (Fig. 4) than recently unburned points (3-6 survey years after fire). In populations D and F,

which have the highest frequency of fire (Fig. 2), these differences are in the same direction but not significantly different (Fig. 4).

## DISCUSSION

The 16-year fire regime we have described within Cape Sable seaside sparrow habitat is consistent with what has previously been reported for the entire Everglades ecosystem for the 45 years prior (Gunderson and Snyder, 1994). Moreover, we have evidence that even areas with the highest occupancy rates have burned extensively during the span of our 16-year record. Thus, fire clearly is a regular driver of Cape Sable Seaside Sparrow population dynamics and there is no reason to suspect that the subspecies has experienced any different fire regimes than have the rest of the inhabitants of the ecosystem. Nevertheless, all available evidence thus far suggests that fire has an initial negative impact on sparrows. Previous local-scale studies have found that burned habitat is not used for two years following fire, and that no birds directly affected by the burn have ever been resighted afterwards (La Puma et al. 2007; Werner 1975; Werner and Wolfenden 1983). Our results are consistent with the prior work, in that they show site occupancy is significantly lower in the first two years following fire across the entire range of the subspecies. Additionally, our longer period of record indicates that occupancy may take as many as 10 years to reach the maximum levels observed.

None of the fire specific variables (i.e. fire size, seasonality, soil depth) we considered were able to explain observed variability in the site occupancy among survey

points in the first two years after a fire event, despite their putative importance (Taylor 1983; Werner 1975). Our failure to find a link between occupancy during the first two years post fire, and fire characteristics, may indicate that these variables are indeed unimportant at this scale of observation. It is also possible that our variables were too coarse in scale to provide a strong connection between sparrow site occupancy and fire traits. There is certainly room for further exploration of the role these characteristics play in the recovery rate of Cape Sable Seaside Sparrows after a fire event.

Despite the evidence that sparrow numbers are reduced by fire, our analyses show an apparent asymptote in occupancy at 10 years post-fire followed by a decline down to below the unburned average. This finding is consistent with the early research of Taylor (1983) and Werner (1975) and suggests a potential for sparrow habitat to transition into a state unsuitable for use after a long fire-free interval. Our results suggest at least a 10-year fire return interval would be beneficial for maintaining productive sparrow habitat, which is longer than either Werner or Taylor's recommendation for a 4-year fire return interval. However, our result is congruent with the results of Gunderson and Snyder (1994) who show that episodic large fires occur on the order of every 10-14 years. Nevertheless, we must temper this conclusion with the realization that our results are correlational only. In other words, we cannot ascribe a mechanism to the lack of sparrows found in survey sites that have not burned in over 10 years. It is quite possible, for example, that these are the same sites that experience wetter than average conditions throughout the year, do not burn often because of higher average water conditions, and are suboptimal sparrow habitat because of the effects of water flow and not fire.

This potential confounding relationship is illustrated within population C. Cassey et al. (2007) showed that occupancy in this population has increased annually since the late 1990s. Yet we show that points that have not burned for 12+ years have lower site occupancy than points that have burned more recently (Fig. 4a). Thus points that have not been burned for 12+ years are clearly not those points that are being used by sparrows. In fact, the points that have not burned for 12+ years are also the points that lie closest (directly adjacent) to Taylor Slough and thus are also the points that are experiencing relatively longer hydroperiods and deeper water levels. From our analyses, we cannot determine whether the lack of fire or the effects of high water are precluding sparrows from using these sites.

Although fire is clearly a part of the sparrow's evolutionary history, we must employ extreme caution when couching our results in the context of Cape Sable Seaside Sparrow management. Cape Sable Seaside Sparrows occur in six disjunct populations, four of which are at critically low numbers, and the two largest of which are located only kilometers from each other. Because of this, sparrow recovery is dependent on the exclusion of even relatively small-scale fire events, as these occurrences represent a threat to the persistence of the subspecies. Thus, at least over the near term, we cannot allow fire to run its natural course without imposing management safeguards to protect the subspecies.

The increase in sparrow occupancy after two years post-fire is evinced in all populations with the exception of population A. Population A is the only one to have experienced a significant ongoing decline in sparrow occupancy since 1992 (Cassey et al. 2007). In addition population A has only experienced four fire events at survey points (two in 1993 and one each in 2003 and 2004). It has been previously well documented that the decline in sparrow occupancy in population A is due to flooding (Pimm et al. 2002).

In both populations D and F, fires are burning at such a high frequency (every two to four years) that sparrows may be continually excluded from available habitat. These two populations have burned over 100% of their spatial extent since 1989. Both lie at the interface between ENP and greater Miami, which is a boundary that is commonly subjected to fires that start outside the park boundary. Indeed, unlike all other populations, F has burned more area in the dry season than in the wet, likely as a consequence of arson fires that start across the ENP boundary and readily spread into the park (and sparrow habitat) given the very dry conditions of the season. Population D, on the other hand, follows the general trend observed across sparrow habitat of burning predominately in the wet season, yet the extent to which it has burned still remains well above the mean for the populations within fire-prone regions of the park (i.e. excluding A). Finally, although site occupancy does increase following the first two yearly surveys after a fire event, unlike in the other populations with less frequent fire events (B, C, E), this increase is not statistically significant in either F or D. Together these results argue for a role of fire in the decline and non-recovery of these small sparrow populations (Cassey et al. 2007), since they may not be of sufficient size to endure fires at the frequency and extent they have experienced in the recent past.

We can extend this concern about the adverse effect of fire to the larger populations of B and E as well. These two populations are within kilometers of one another at their closest point (Fig. 1). While annual small lightning-ignited or prescribed fires likely have negligible long-term effects on the sparrows in these populations, the size and shape of both the fire and the population's geographic extent will undoubtedly influence the degree to which a fire has lingering negative effects. For example, one large episodic fire like the

Ingraham Fire of 1989 will have a catastrophic impact on the entire subspecies, given its current aggregated distribution.

## **CONCLUSIONS**

Our analysis has taken information about patterns of Cape Sable Seaside Sparrow habitat occupancy (Pimm et al. 2002; Taylor 1983; Werner 1975), and about how sparrows respond to fire (La Puma et al. 2007), and combined them within the landscape context of the recent fire history of the Everglades. We found evidence for an initial significant negative impact of fire on sparrow occupancy that persists for two years across the sparrow's entire current range, after which we show site occupancy begins to resemble values typical of unburned habitat. The sparrow's immediate response to fire is quite variable, which is likely due to the landscape heterogeneity and the stochastic nature of disturbance regimes (including flooding regimes). Nevertheless, none of our fire- or site-characteristic variables explained differences in site occupancy immediately after fire events. We suspect that too frequent fires are contributing to the loss of sparrows in the two populations closest to the wildland/urban interface. We provide some evidence that sparrows do not occupy habitat that has not burned for long periods (>12 years), however we cannot rule out the possibility that this pattern is confounded with other factors that may be driving sparrows out of these sites (e.g., relatively high water flows). Management of the species is complicated by drastic declines in density and spatial extent over the past two decades. Thus, our results suggest that fire, although a natural part of the landscape, must be carefully managed within the remaining occupied portions of Cape Sable Seaside Sparrow habitat until population numbers are substantially increased to near-historic levels. Because both our population and

landscape-level studies have yet to show any positive influence of fire on sparrow habitat or demography, we do not recommend prescribed burning within sparrow habitat for the sake of increasing habitat suitability. Further research should address critical thresholds for population viability and test further the effect of fire on populations of varying size and spatial orientation. In sites where once suitable habitat has clearly shifted to an unsuitable community (in all cases this appears to be due to hydrological effects), prescribed fire should be used as an experimental tool to determine its value as a restorative mechanism.



## **ACKNOWLEDGEMENTS**

The authors would like to thank the United States National Park Service for providing funding to JLL under the Critical Ecosystems Studies Initiative; Sonny Bass for providing the range-wide survey data and his team of biologists for their efforts conducting the survey over the years; the many members of Everglades Fire Management who collected data for each fire; and the ENP aviation safety crew for keeping everyone safe while traversing Everglades National Park. We would also like to thank Benjamin Baiser for his work on determining wet-season onset date; and Julian Avery, David Ehrenfeld, Blake Mathys, and Greg Shriver, for making constructive comments on the manuscript prior to submission.

## LITERATURE CITED

- Beckage B., Comiskey J. and Duke-Sylvester S. 2005. Natural fire regimes in southern Florida - Response. *Natural Areas Journal* 25: 6-8.
- Beckage B., Platt W.J., Slocum M.G. and Panko B. 2003. Influence of the El Nino Southern Oscillation on fire regimes in the Florida everglades. *Ecology* 84: 3124-3130.
- Brawn J.D., Robinson S.K. and Thompson Iii F.R. 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics* 32: 251-276.
- Cassey P., Lockwood J.L. and Fenn K.H. 2007. Using long-term occupancy information to inform the management of Cape Sable Seaside Sparrows in the Everglades. *Biological Conservation* 139: 139-149.
- Curnutt J.L., Mayer A.L., Brooks T.M., Manne L., Bass O.L., Jr., Fleming D.M., Nott M.P. and Pimm S.L. 1998. Population dynamics of the endangered Cape Sable seaside-sparrow. *Animal Conservation* 1: 11-21.
- Gunderson L.H. and Snyder J.R. 1994. Fire patterns in the southern Everglades. *In* Davis S. M. and Ogden J. C. (eds.), *Everglades: the ecosystem and its restoration*, pp. 291-306. St. Lucie Press, Delray Beach, FL.
- Hastings A. 2003. Metapopulation Persistence with Age-Dependent Disturbance or Succession. pp. 1525-1526. *American Association for the Advancement of Science*.
- Hunter W.C., Buehler D.A., Canterbury R.A., Confer J.L. and Hamel P.B. 2001. Conservation of Disturbance-Dependent Birds in Eastern North America. *Wildlife Society Bulletin* 29: 440-455.

- Jenkins C.N., Powell R.D., Bass O.L. and Pimm S.L. 2003. Demonstrating the destruction of the habitat of the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). *Animal Conservation* 6: 29-38.
- Kushlan J.A. and Bass Jr O.L. 1983. Habitat use and the distribution of the Cape Sable Sparrow. *The Seaside Sparrow: Its biology and management* (TL Quay, JB Funderburg, Jr., DS Lee, EF Potter, and CS Robbins, Eds.). North Carolina Biological Survey Occasional Paper 5: 139–146.
- La Puma D.A., Lockwood J.L. and Davis M.J. 2007. Endangered species management requires a new look at the benefit of fire: The Cape Sable Seaside Sparrow in the Everglades ecosystem. *Biological Conservation* 136: 398-407.
- Lande R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. *The American Naturalist* 142: 911-927.
- Levin S. and Paine R. 1974. Disturbance, Patch Formation, and Community Structure. *Proceedings of the National Academy of Sciences* 71: 2744-2747.
- Lockwood J.L., Davis M. and La Puma D.A. 2003a. Fire effects on Cape Sable Seaside Sparrow demography: year two. Unpublished report. University of Santa Cruz, Santa Cruz, California.
- Lockwood J.L., Ross M.S. and Sah J.P. 2003b. Smoke on the water: the interplay of fire and water flow on Everglades restoration. *Frontiers in Ecology and the Environment* 1: 462-468.
- MacKenzie D.I., Nichols J.D., Lachman G.B., Droege S., Royle J.A. and Langtimm C.A. 2002. Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One. *Ecology* 83: 2248-2255.

- Martin J., Nichols J.D., Kitchens W.M. and Hines J.E. 2006. Multiscale patterns of movement in fragmented landscapes and consequences on demography of the snail kite in Florida. *Journal of Animal Ecology* 75: 527-539.
- Nott M.P., Bass O.L., Jr., Fleming D.M., Killeffer S.E., Fraley N., Manne L., Curnutt J.L., Brooks T.M., Powell R. and Pimm S.L. 1998. Water levels, rapid vegetational changes, and the endangered Cape Sable seaside-sparrow. *Animal Conservation* 1: 23-32.
- Pickett S.T.A. and White P.S. (eds.) 1986. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, San Diego, CA.
- Pimm S.L., Lockwood J.L., Jenkins C.N., Curnutt J.L., Nott M.P., Powell R.D. and Oron L. Bass J. 2002. Sparrow in the grass: a report on the first ten years of research on the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). Report to the National Park Service. Everglades National Park, FL.
- Platt W.J., Beckage B., Doren R.F. and Slater H.H. 2002. Interactions of large-scale disturbances: Prior fire regimes and hurricane mortality of savanna pines. *Ecology* 83: 1566-1572.
- Ross M.S., Sah J.P., Ruiz P.L., Jones D.T., Cooley H., Travieso R., Tobias F., Snyder J.R. and Hagyard D. 2007. Effect of Hydrologic Restoration on the Habitat of the Cape Sable Seaside Sparrow-Annual Report of 2005-2006 for Everglades National Park: Miami. FL, Southeast Environmental Research Center, Florida International University 46.
- Slocum M.G., Platt W.J., Beckage B., Panko B. and Lushine J.B. 2007. Decoupling natural and anthropogenic fire regimes: A case study in Everglades National Park, Florida. *Natural Areas Journal* 27: 41-55.

- Sousa W.P. 1984. The Role of Disturbance in Natural Communities. *Annual Review of Ecology and Systematics* 15: 353-391.
- Taylor D.L. 1983. Fire Management and the Cape Sable Sparrow. *North Carolina Biological Survey and North Carolina State Museum, North Carolina*. pp. 147 - 152.
- Walters J.R., Beissinger S.R., Fitzpatrick J.W., Greenberg R., Nichols J.D., Pulliam H.R. and Winkler D.W. 2000. The AOU Conservation Committee review of the biology, status, and management of Cape Sable Seaside Sparrows: Final report. *Auk* 117: 1093-1114.
- Werner H. 1975. The Biology of the Cape Sable Seaside Sparrow. *Everglades National Park, Homestead*.
- Werner H.W. and Wolfenden G.E. 1983. The Cape Sable Sparrow: its habitat, habits, and history. *The Seaside Sparrow, its biology and management. North Carolina Biological Survey and North Carolina State Museum*.

## LIST OF TABLES

**Table 1.** Area (in hectares) of spatial extent burned (SEB) and total area burned (TAB) for each population from 1989 – 2005 (see text for definitions). Also included are the percentages of the total geographical extent of each population that burned calculated using SEB or TAB, given both as annual estimates and over the entire period of record.

	Area	of	%	% SEB		% TAB	
Population	Population	SEB	SEB	annually	TAB	% TAB	annually
A	23,588	3,220	14%	0.90%	3,372	14%	0.90%
B	14,191	8,630	61%	4.00%	15,102	106%	6.70%
C	2,882	2,031	70%	4.40%	3,073	107%	6.70%
D	2,901	2,287	79%	5.00%	3,643	126%	7.90%
E	7,225	6,040	84%	5.20%	7,503	104%	6.50%
F	2,673	2,287	86%	5.40%	4,264	160%	10.00%

**Table 2.** Univariate models for the relationship between Cape Sable Seaside Sparrow site occupancy one-year post-fire and four characteristics of the fire. Categorical estimates for fire type and season are interpreted as relative to ‘Prescribed’ burns and ‘Wet’ season respectively. Linear estimates were produced from a binomial logistic mixed model that included year and controlled for nested population structure as random effects.

Variable	Burned points	Measurement	Estimate	std err	t-statistic	P-value
Fire extent	71	Log <sub>10</sub> (hectares)	0.79	0.74	1.06	0.292
Fire type	71	Human	1.87	1.97	0.95	0.347
		Lightening	-0.01	0.79	-0.01	0.995
Season	71	Dry	1.89	1.96	0.96	0.339
Soil depth	50	(cm)	0.08	0.08	0.98	0.33

## FIGURE LEGENDS

**Fig. 1.** Map of Everglades National Park in south Florida, showing locations of six extant populations of the Cape Sable Seaside Sparrow (area with diagonal line fill), and perimeter of fire within population E that was studied by La Puma et al. (2007; white with black outline).

**Fig. 2.** The frequency with which range-wide survey points, that have ever held sparrows, have burned up to four times during the period of record (1989 – 2005), by population. Population A has the fewest burned points, whereas D and F have the greatest proportion of points that burned more than twice.

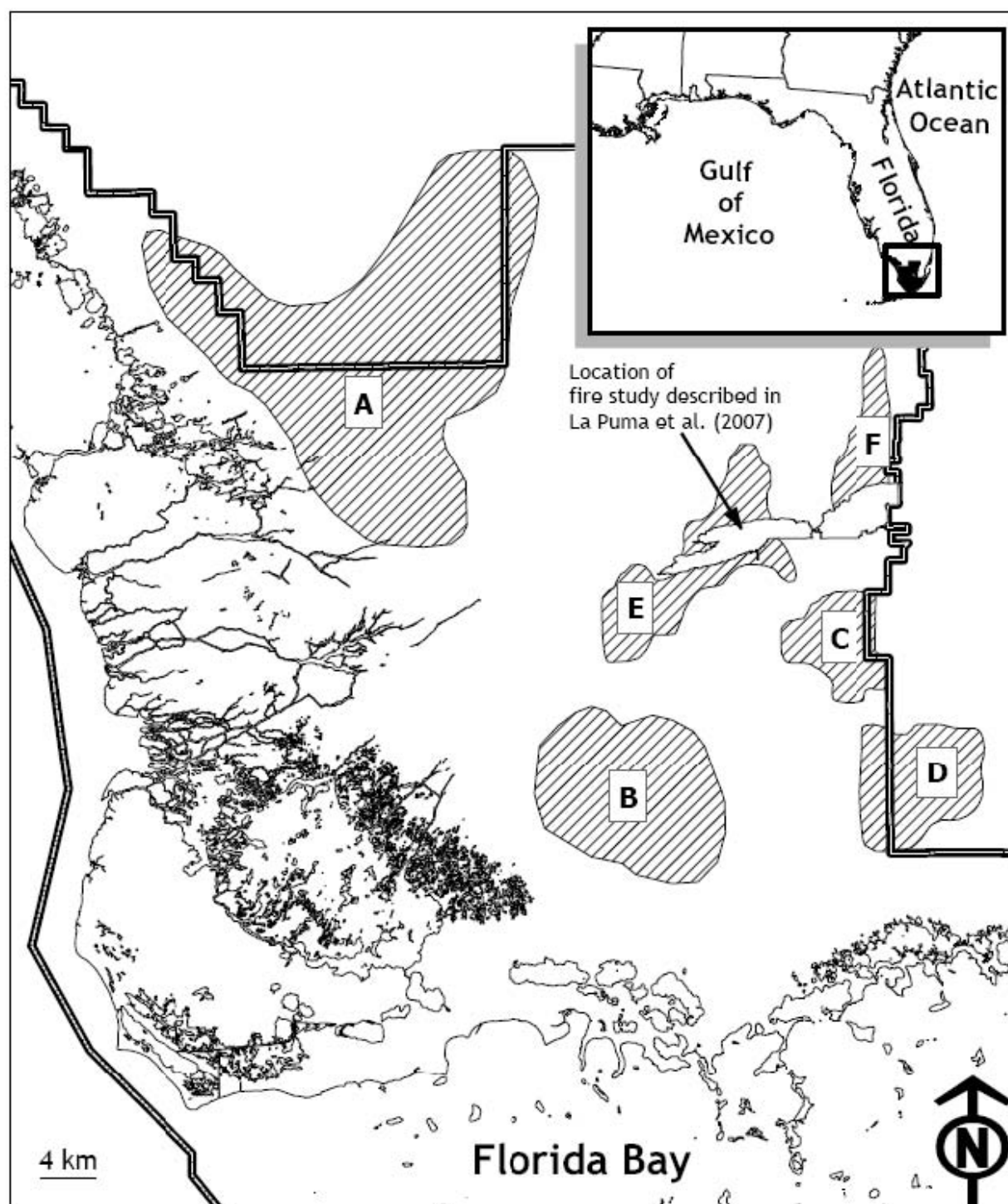
**Fig. 3.** Probability of site occupancy by Cape Sable Seaside Sparrows following known fire events during the 16 years ranging from 1989 – 2005. Error bars around each estimate are  $\pm 1$  SE and were calculate using the Delta method to back-transform estimates. The dotted line is the average site occupancy for all frequently surveyed points (i.e. those surveyed at least six times), which are known to have been occupied by sparrows (i.e. have had at least on sparrow detection) and have never burned during the study period. The fitted line is the logistic quadratic  $P(\Psi) = -1.83 + 0.20TSF + -0.01TSF^2$ .

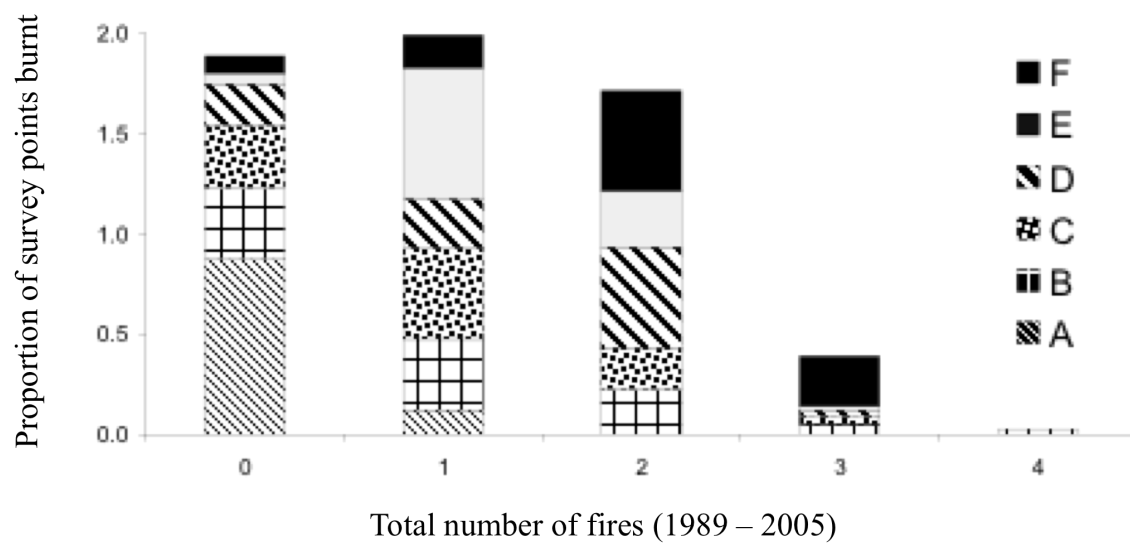
**Fig. 4.** Probability of site occupancy by Cape Sable Seaside Sparrows in annual range-wide surveys following known fire events for a) the small populations (A = solid square, C = hollow square, D = hollow triangle, F = hollow diamond) and b) the large subpopulations (B

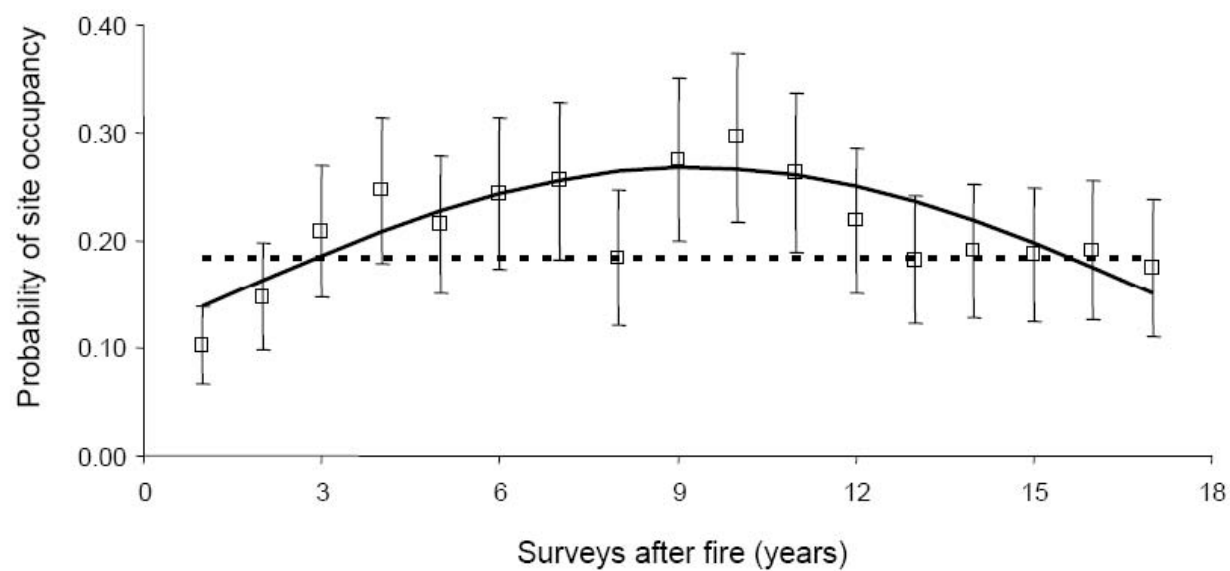


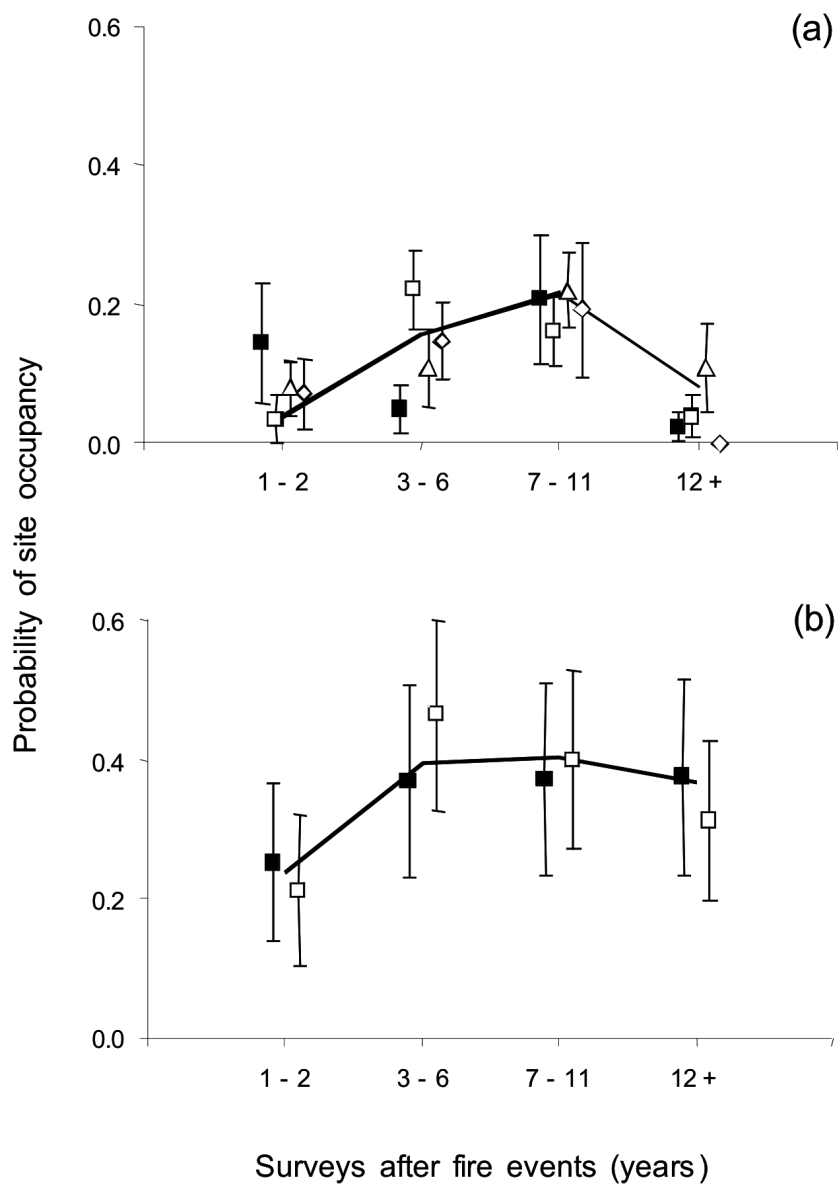
= solid square, E = hollow square). Because of differences in fire frequencies between populations, time-since-fire was binned into four successive intervals. Occupancy increases over the first two bins in all populations except A (see results). In populations B (estimate  $\pm$  std err =  $0.55 \pm 0.20$ ,  $t = 2.74$ ,  $P = 0.006$ ), C (estimate  $\pm$  std err =  $2.05 \pm 1.00$ ,  $t = 2.05$ ,  $P = 0.041$ ), and E (estimate  $\pm$  std err =  $1.16 \pm 0.46$ ,  $t = 2.54$ ,  $P = 0.011$ ) these increases are significantly greater in the second interval of time-since-fire over the first. The average trends in occupancy (excluding population A) are quadratic models for time-since-fire across the entire survey period plotted at the midpoint of each of the four bins. All models control for the effect of year and quad (see methods).

Figure 1.



**Figure 2.**

**Figure 3.**

**Figure 4.**

## Chapter 3

# **DETERMINING THE STATISTICAL POWER OF DETECTING DECLINES IN OCCUPANCY AND ABUNDANCE OF THE CAPE SABLE SEASIDE SPARROW (*AMMODRAMUS MARITIMUS MIRABILIS*)**

David A. La Puma<sup>\*</sup>, Kenneth Elgersma, Julie L. Lockwood

## **SUMMARY**

1. Endangered species management requires monitoring methods that can detect important biological changes over short time periods.
2. Long-term datasets can provide insight into the statistical power of existing monitoring protocols. By fitting such data to statistical models that account for excess variation, managers can derive meaningful parameter estimates about the distribution of survey data.
3. By simulating population change scenarios based on the underlying distributions of existing data, managers can consider the power of multiple alternative methods to detect changes in populations.
4. We demonstrate this method using a long-term data set for the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) in Everglades National Park, USA.
5. Our results demonstrate that the current survey protocols are unable to detect even large declines over short time periods (3 years) but improve with additional years of data (5-10 years).
6. Differences were minimal between occupancy and abundance, and between linear versus logistic declines, over the various time periods we considered.

7. Given that monitoring data exist for many species, and the widespread interest in adaptively managing large ecosystems, this method will prove useful for managers to assess current protocols, as well as to evaluate future monitoring alternatives.

**KEYWORDS**

abundance, endangered species, monitoring, occupancy, power, zero-inflated Poisson

## INTRODUCTION

Agencies charged with the conservation of endangered species are obligated to choose monitoring methods that can detect biologically important changes over time intervals that are small enough to mitigate further declines. Because of limited conservation dollars, these protocols must balance the type of information desired with the financial and logistical constraints of the managing agency. No matter the protocol adopted, there are tradeoffs between the information gained and the time and effort required to collect needed data. While many agencies desire estimates of current abundance, the decision to implement a conservation action are most often based on thresholds of decline. For example, the IUCN established protocols for listing threatened and endangered species based on the rate of decline in population size or site occupancy over fixed time periods (Bubb et al. 2009; Butchart et al. 2004). Many agencies impose their own management triggers based on declines deemed important for their specific goals (Hatch 2003; Seavy and Reynolds 2007). Therefore, when choosing a monitoring protocol, managers must also consider the ability of a method to detect what they deem are biologically important changes in their species of interest.

Setting clear monitoring objectives forces managers to consider the response of the species being monitored to management actions and/or natural phenomena of interest (Romesburg 1981). Often, though, monitoring protocols are developed without clear objectives, yet with the expectation that they will answer myriad management questions as they arise (Yoccoz et al. 2001). Such methods often come at a cost in terms of statistical inference, since *a posteriori* hypotheses are much more difficult to test (Nichols 2001; Steidl et al. 1997; Williams et al. 2002) Despite the inherent issues in such an approach, these



databases are maintained because of their perceived value as long-term records for many species. We suggest that one use of such historical monitoring records is as pilot data to inform modifications to an original protocol so that it is updated to current scientific standards while also maintaining the integrity of the long-term records. In this sense, long-term datasets can provide robust information on the structure of the field data, especially relative to the presence and influence of excess variation in occurrence data characteristic of rare or elusive species. By properly modeling such data, investigators can obtain parameter estimates with which to simulate population declines and determine the power of various protocols to best detect such declines (Joseph et al. 2009; Joseph et al. 2006b; Sims et al. 2008b; Sims et al. 2006). Here we demonstrate how parameter estimates derived from existing monitoring data on the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) can be used to evaluate the statistical power of a long-term survey to detect population declines of various magnitudes.

The Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), a subspecies of the seaside sparrow, is one of many globally threatened and endangered birds for which measures are being taken to prevent extinction. The sparrow resides in the dynamic short-hydroperiod prairies of the Everglades ecosystem. This landscape is characterized by patterns of flooding and fire that vary in temporal scale from days to decades (Davis and Ogden 1994). Efforts to restore natural water flows to the Everglades ecosystem are currently underway as part of the multi-billion dollar Comprehensive Everglades Restoration Plan (CERP). Several elements to this restoration plan have already been implemented with other projects set for implementation in the coming years (CERP 2008). Evaluating the effectiveness of the Everglades restoration depends on proper use of adaptive management

techniques (Recover 2008), which principally includes the response of constituent species to the various restoration actions (Cade and Dong 2008). From the standpoint of Cape Sable seaside sparrow recovery efforts, managers must be able to evaluate whether (and to what extent) restoration efforts have had a positive impact on sparrow abundance and occupancy either through reduced flooding of habitat or decreased unseasonal fire activity. Alternatively, there is the possibility that restoring water flows to portions of the Everglades ecosystem will have inadvertent consequences on sparrow populations, such as flooding occupied habitat and reducing the availability of nesting sites. In order to successfully accomplish Everglades restoration, managers must have a monitoring protocol that is powerful enough to detect biologically important changes in the current sparrow population within a timeframe that allows them to modify their management activities appropriately.

The current monitoring protocols for Cape Sable seaside sparrows were developed in 1981, with a primary goal being to map the distribution of sparrows across the ecosystem (Kushlan and Bass 1983). Since then the information gathered has been used to estimate population size, as well as to determine whether individual sparrow subpopulations are declining (Pimm et al. 2002). Walters et al. (2000) questioned the ability of the current survey to detect changes in the population primarily because the protocol lacked within-year replication, which precludes the calculation of detection probability. Detection probability has been shown to be vitally important when estimating abundance and/or occupancy (Mackenzie et al. 2005). In addition, since the total population has declined by over 60% since 1992 (Curnutt et al. 1998; Nott et al. 1998; Pimm et al. 2002), thus leaving only a fraction of the total range still occupied, it is not clear if the current survey protocol has the power to detect any further declines.

With these issues in mind, we address three key questions. First, what statistical distribution best captures the variability in numbers of sparrows counted within a single year? Using this information we then ask, what is the power of the current survey to detect meaningful biological changes in sparrow abundance? Finally we ask what gain in power, if any, can be achieved by choosing occupancy over abundance as our response variable?

## **METHODS**

### *Study Species and Survey Protocol*

The Cape Sable seaside sparrow was listed as ‘endangered’ under the US Endangered Species Preservation Act of 1967 due to its limited distribution and threats of habitat conversion by agricultural practices (Pimm et al. 2002). The sparrow was then included in the first Endangered Species Act of 1973, and has remained a listed species ever since. The sparrow is endemic to the short-hydroperiod (< 7 months underwater) marl prairies of the Everglades ecosystem of South Florida. The sparrow occupies a subset of this ecotype; that which is < 40m from emergent woody vegetation (Jenkins et al. 2003a, b) and where water levels do not preclude the vegetation structure necessary for nesting (Lockwood et al. 2001). Therefore, of the total extent of marl prairie, the Cape Sable seaside sparrow is known to occupy a subset of roughly 80 km<sup>2</sup>. The overall sparrow population was subdivided into six geographically discrete subpopulations (A – F) by Curnutt et al. (1998; Figure 1). While there is evidence that individual birds do move between subpopulations, these occurrences are rare compared to the strong site fidelity that typifies the subspecies (Boulton et al. 2009) thus affirming that these subpopulation designations are biologically meaningful.

The Everglades ecosystem has undergone severe fragmentation relative to its historical pattern of water flow (Sklar et al. 2001). This fragmentation has led to each sparrow subpopulation experiencing flood and fire conditions that are relatively independent of the others (La Puma et al. in prep.). The end result is that each sparrow subpopulation has tended to follow a unique abundance and occupancy trajectory (Cassey et al. 2007). Work by Pimm et al. (2002) has shown that water management coupled with several years of severe precipitation, have lead to >90% decline in abundance within subpopulation A, which was the second largest subpopulation in the 1981 and 1992 surveys. In subpopulation B, in comparison, the number of individuals detected has remained consistent over this same time period. Of all the populations, subpopulation C is the only one that has shown any tendency towards rebounding in area occupied with an increase in occupancy between 1992 and 2005 (Cassey et al. 2007). Two of the subpopulations (B & E) now account for over 95% of the total number of sparrows recorded, leaving the remaining 5% divided between the other four subpopulations. For this reason hereafter we refer to subpopulations B and E as the “large” subpopulations, while we refer to the rest as the “small” subpopulations.

Since 1992, park biologists have conducted annual point count surveys along a 1km grid laid across the entire range of the subspecies (Curnutt et al. 1998). Surveys begin in early April, during peak sparrow breeding season, and usually conclude after one month. Surveys begin 30mins after civil twilight and end around 08h30m. Researchers are transported to survey points via helicopter, dropped off in succession along the 1km grid, and retrieved 10 minutes later. Each researcher conducts fixed-radius point counts for the first seven minutes that they are on the ground, beginning after helicopter noise has subsided. All sparrow individuals heard singing within a 200-meter radius are recorded. Point counts are

restricted to non-windy and precipitation-free days. Full details of the survey method can be found in Curnutt et al. (Curnutt et al. 1998).

### *Model Fit and Power Simulations*

Our goal was to use this existing 15-years of survey information (1992-2007) to parameterize simulations of future population declines. By simulating population declines in this way, we tested the ability of the current survey methodology to detect declines of various magnitudes. This work was carried out in three steps. First, we fit the survey data to both standard and zero-inflated Poisson models in order to determine whether the zero-inflation provided a better fit to the observed count data. Second, once we determined which model fit was best, we tested the fit of the data to a nested series of models of that type, to determine which combination best fit the data. In the third step, we used parameter estimates (i.e. mean and variance) from the best-fit model to parameterize our simulations of population declines. We simulated declines in abundance and in occupancy to determine whether either response variable provided more power to detect declines across our range of scenarios. Each of these steps is detailed below.

### *Model Selection*

A histogram of our entire dataset revealed that, besides a high number of zeroes (no birds detected), the general shape of our data resembles a Poisson distribution (Figure 2). This pattern holds up at the individual population level as well (Figure 3). The Poisson is also the distribution that is most typically used to model count data (Zar 1998).

<Figure 2 about here>

<Figure 3 about here>

When faced with excess zeroes in their data, many researchers adopt a standard distribution (such as a Poisson) and then add one or more normally-distributed error terms as a means for increasing the variance (Seavy and Reynolds 2007; Sims et al. 2008a; Sims et al. 2006). We took a different approach in that we opted to fit our data to both standard and zero-inflated Poisson distributions, with time (year) and space (subpopulation) as possible covariates. Whereas the standard Poisson model assumes that all zeroes arise from the same process, the zero-inflated Poisson model is a class of mixture models that assumes zero values arise from either real absences (i.e. there is no bird residing at a survey point; this is comparable to the standard Poisson) or they arise from a false non-detection (i.e. a bird was there, but the observer did not detect it). The first probability is modeled via a Poisson distribution, whereas the second (the detection probability) is modeled as a binomial random process (Lambert 1992; Welsh et al. 1996). Using the glm procedure from the R library ‘stats’ (R Development Core Team 2009), we assessed the fit of a standard Poisson model to the full sparrow survey data (all counts across all years), while including both year and subpopulation as regressors. The inclusion of these regressors thus acknowledges the known drop in sparrow abundance within the time frame in which the data were collected, and the known differences in abundance of sparrows across subpopulations. Using the R library ‘pscl’, we then fit the same dataset to a zero-inflated Poisson model including the same regressors (Zeileis et al. 2008).

We compared the standard Poisson model to the zero-inflated Poisson using a Vuong Non-Nested Hypothesis Test (R library ‘pscl’). This test compares the predicted probabilities of two models that do not nest, such as between a zero-inflated Poisson model and its

standard Poisson analog (Jackman 2008). The null hypothesis ( $H_0$ ) for this test is that there is no difference between the standard and zero-inflated Poisson models. A large positive test statistic in this case indicates support for model 1 (standard Poisson) over model 2 (zero-inflated Poisson), where a large negative test statistic indicates more support for model 2 over 1.

We next utilized a model-fitting process to derive meaningful estimates of variance about mean estimates of abundance and occupancy that could be used to create simulated future declines in these metrics. These simulations are our basis for calculating power (see below). Based on the results of the Vuong test, which indicated that the zero-inflated Poisson distribution was more appropriate for our dataset (see Results), we then fit our data to a series of nested zero-inflated Poisson models. We assumed that our count data would be best explained by year, since the majority of the subpopulations have declined over the period of record. We also considered that the excess zeroes would be caused by subpopulation, since the subpopulations represent variation in sparrow density that we expected would influence detectability (Lovett-Doust et al. 2009; Royle and Nichols 2003; Royle et al. 2005). Therefore, in our global model we included both year and subpopulation as regressors for the number of sparrows counted (the Poisson part of the model), and subpopulation as a regressor for the zero component (the binomial part of the model). All candidate models were evaluated using Akaike's Information Criterion AIC, and the model with the lowest AIC score was retained to parameterize our power analysis simulations.

### *Power Analysis*

Statistical power can be defined as  $1-\beta$ , where  $\beta$  is the probability of committing type II error; that is, not rejecting the null hypothesis when in fact it is false. Therefore, statistical power represents the probability of correctly rejecting the null hypothesis when it is false (Table 1).

<Table 1 about here>

Power is comprised of four elements: effect size (ES), precision ( $\alpha$ ), sample size (n) and the standard deviation about the sample mean ( $\sigma$ ) (Cohen 1988). Therefore, we can express power as an equation incorporating all of these elements as:

$$\text{Power} \approx \text{ES} * \alpha * \sqrt{n} / \sigma \quad \text{eqn 1}$$

Equation 1 suggests that increasing the effect size and/or the sample size will increase power, while increasing the alpha value or increasing the sample variance will lower it. Based on these relationships, we made several *a priori* decisions before creating simulations of our data to determine the power of our current sparrow survey.

We were interested in determining the power of the current survey to detect both short and long-term changes in sparrow abundance or occupancy. We therefore choose three time periods over which we might expect this survey to produce meaningful feedback on management decisions, which were 3, 5 and 10 years. Detecting a three-year decline represents our best-case scenario, since three years is the minimum statistical requirement for detecting a trend. Five years, represents a standard period over which many management activities and experimental manipulations are judged (Pimm 1991). Thus, one expectation is that sparrow monitoring protocols should be powerful enough to detect moderate to small 5-year declines within subpopulations, as well as small declines across the sparrow's total



range. The 10-year period represents long-term feedback on how the sparrow is faring. Given the already low population estimates for the sparrow, we suggest that the 10-year time span is likely not useful as feedback for adaptive management purposes. However, this is a standard time frame by which the IUCN evaluates species for red-list consideration (IUCN 2001) and thus does provide feedback on whether USFWS recovery goals are being met (United States Fish and Wildlife Service 1999).

Over each of these three periods (3, 5, and 10 years), we simulated a population decline ranging from 10-95%. Because we set out to determine the overall sensitivity of the current survey, we chose a broad range of effect sizes to evaluate. Several points along this continuum, however, are of particular interest. For instance, we would expect to be able to detect small to moderate declines in 10 years, and larger declines over short periods, simply because of the relationship between effect size, sample size, and power. Additionally, this range of declines is well within the historical fluctuations of the sparrow population, as we have seen range-wide population and subpopulation declines of >90% in three years, as well as small (<20%) declines over longer periods (subpopulation B) (Pimm et al. 2002).

In the context of sparrow management, alpha represents the probability that one finds evidence of a decline in sparrows when in fact they have not declined (Table 1). Type I errors, therefore, carry the risk of instigating costly management actions to be implemented when they are not needed. The tradeoff, however, is that by relaxing the alpha value, we increase our power to detect a decline, when one actually exists (see power calculation above). For our simulations, we set our  $\alpha = 0.1$  because it reduces the risk of failing to detect a biologically significant decline, which is considered an outcome of far more of

concern for an endangered species than falsely detecting one that does not exist (Gerrodette 1987).

We set our sample size ( $n$ ) at 381 total survey points, spread proportional to total area encompassed within each of the six subpopulations (A=75, B=144, C=36, D=28, E=73, F=25). This represents the actual number of points surveyed in 2006, except for in subpopulation A. We reduced the number of survey points in subpopulation A because so few of them have actually held birds since 2001. For instance, in 2006, 196 points were surveyed in subpopulation A, yet no more than eight individual sparrows (mean = 5.6) have been detected in subpopulation A since 2001. Therefore, assigning a large number of survey points to subpopulation A would artificially inflate the power in our simulations (power increases with sample size). Therefore, we reduced the number to the minimum number of points surveyed since 2001.

Our variance estimates were derived from our highest-ranked zero-inflated Poisson model (see Results) in order to simulate sparrow populations and declines. Variance must be either calculated directly from empirical data, or estimated based on assumptions about the distribution of the data. In the case of a standard Poisson distribution, variance and mean are equal and represented by the parameter lambda ( $\lambda$ ). Because we are using a zero-inflated Poisson model, each simulated dataset is a product of two random processes; a Poisson random process simulating the count values using the parameter  $\lambda$ , and a binomial random process simulating the amount of zero-inflation using the parameter  $\theta$ . Because year is our regressor for the number of birds counted within our zero-inflated Poisson model, for each year we can calculate an individual value for  $\lambda$ . Since we were interested in simulating population change from the current state of the species, we chose from our model the  $\lambda$  value

corresponding to the year 2007, the last year a complete survey was carried out. Because our model predicted that zero-inflation is best explained by subpopulation, we used the  $\theta$  values for each subpopulation to simulate the number of false absences (zero-inflation) for the respective number of points.

Species declines may occur for many reasons. For instance, in previous work we have shown fire to cause immediate reductions in sparrow abundance and site occupancy in direct relation to the size of the area burned (La Puma et al. in prep.). If we carry this effect over multiple years, we would expect such a decline to be linear in shape. However, population declines due to reductions in fecundity have the effect of reducing abundance proportionally rather than absolutely, as adult sparrows persist for several years while less new birds are produced. Therefore, we would expect such a decline to be logistic in shape. We simulated both linear and logistic declines in sparrows to evaluate the power of the survey to detect each of possibility.

We used the maximum likelihood estimates from the fitted model for  $\lambda$  and  $\theta$  in each subpopulation for the year 2007 to simulate our survey results (R version 2.9.0, R Core Development Team). Each simulated dataset is represented by a  $i*j$  matrix, where  $i$  is a survey point (1,2,3... $i$ ) and  $j$  is time in years (1,2,3... $i$ ). Each cell in this matrix is a data point  $d_{ij}$ , and thus represents the simulated number of sparrows detected at survey point  $i$  of year  $j$ . Since we are simulating our populations from a zero-inflated Poisson model, each data point is a product of two random variables,  $\lambda$ , and a  $\theta$ . In figure 4 we present a schematic example of how the mixture of two random processes generates a set of data values. This construction implies a constant zero-inflation over time, but allows for different zero-inflation values for each subpopulation.

To generate annual population declines, we reduce  $\lambda$  for each year in the simulation by either a fixed percentage (to mimic a linear decline) or a compounded percentage (to mimic a logistic decline). For instance, to simulate a three-year linear decline of 75%, we reduced  $\lambda$  by 0.25 in the first year to get  $\lambda_{t+1}$ , 0.5 in the second to get  $\lambda_{t+2}$ , and 0.75 in the third to get  $\lambda_{t+3}$ . On the other hand, to model a logistic decline, we reduced  $\lambda_{t0}$  by 0.63 to get  $\lambda_{t+1}$  then reduced  $\lambda_{t+1}$  by 0.63 to get  $\lambda_{t+2}$  and reduced  $\lambda_{t+2}$  by 0.63 to get  $\lambda_{t+3}$ .

We repeated this procedure 1000 times such that we created 1000  $i*j$  matrices that included all survey points from all subpopulations (the total population; 381 points). For each matrix we then summed all the survey points for each year such that we were left with one matrix of 1000 rows x  $j$  years with values for each year representing the total population and each row representing a time series (i.e. the sum of all plot values  $i$  for that year  $j$ ). We did this for both the total population, and each individual subpopulation separately. We then fit a linear regression to each time series and recorded whether the estimated slope was significantly less than zero (one-tailed test to detect a decline only). Power was then calculated as the proportion of the 1000 regressions in which the slope was significantly less than zero.

<Figure 4 about here>

Finally, we determined whether the binary response variable, occupancy, would provide greater power with which to detect a decline in the sparrow population. It has been previously demonstrated that the variance inherent in count-based abundance data can reduce the power to detect changes in abundance over time (Mackenzie et al. 2005). It has also been demonstrated that in cases where little effort is available for surveys, converting data to presence/absence-based occupancy values can reduce this variance enough to elucidate real

trends in the data (Joseph et al. 2006a). It was our hypothesis that in subpopulations where abundances were very low (small populations), and therefore where survey points were fewer, occupancy would increase our ability to detect a trend of a specific size over the use of count data.

Whereas in the abundance analysis, our zero-inflated Poisson model estimated the proportion of zeroes thought to arise from outside of the Poisson process, in our occupancy simulation we lack a model framework to derive such estimates for detection probability. In order to do so with a zero-inflated binomial (ZIB) model, we require within-year replication of surveys that estimate detection probability. Because we lack any within-year replication, we used two datasets that provide an indication of detection in large and small populations (see appendix). Based on these results, we set the detection probability for the small subpopulations at 0.4, and the two large subpopulations at 0.6. We also note that these values are within the range of those estimated by the zero-inflated Poisson for our abundance analysis (see Results).

In order for us to simulate presence/absence data in a manner consistent with our abundance simulations, we needed a measure of “true” occupancy. To do so, we first converted the simulated count data to presence (1) absence (0) values. The ratio of presences to absences, then, represents “true” occupancy (proportion of sites occupied). We then used the detection probabilities derived for small and large subpopulations (see above) to deflate the number of absences, and inflate the number of presences. This result theoretically represented the “naïve estimate” of occupancy (Mackenzie et al. 2006), or the maximum number of occupied points given that all birds present are detected. We then fit a logistic regression to the presence/absence data using a general linear model, from which we

obtained a probability of occupancy for each subpopulation. As with the zero-inflated Poisson, we simulated 1000 matrices of point count data, but instead, here we used a joint distribution of two random binomial processes, the first representing site occupancy ( $\Psi$ ) and the second the probability of detection ( $\theta$ ; our source of zero-inflation).  $\Psi$  was generated using the maximum likelihood estimator from our logistic regression, while  $\theta$  was assigned based on the size of the population (small = 0.4; large = 0.6). We simulated population declines as in the previous simulations of abundance. Also as with the abundance simulations, detection probability remained constant over all years in our simulation, but was allowed to vary by subpopulation.

## RESULTS

### *Model fitting*

Results from the Vuong test comparing our zero-inflated Poisson model with the ordinary Poisson regression model (test statistic = -18.623) indicated much stronger support for the zero-inflated model ( $p < 0.0001$ ). Thus, we found that the sparrow survey data from 1992 to 2007 is best represented by the zero-inflated Poisson. Our three candidate zero-inflated Poisson models were then evaluated using Akaike Information Criterion (AIC), with the global model showing the greatest support by orders of magnitude (Table 3). Model weights indicated almost no support for either of the two simpler candidate models. The global model included both year and subpopulation as predictors of bird count, and subpopulation as the predictor of excess zeroes. The parameter estimates derived from our best-fit zero-inflated Poisson model (abundance) and logistic regression (occupancy), used for our population simulations, are presented in Table 2.

<Table 2 about here>

<Table 3 about here>

### *Survey Power*

#### *3-year decline*

Our simulation results indicate that the current survey has enough power to detect a 70% linear decline in abundance for the total population. The power to detect a linear decline within any of the subpopulations, however, is low. For example, in order to detect a 3-year decline with 90% confidence, subpopulation B would have to decline by at least 90%, and A and E by at least 95%. The power of the current survey to detect a logistic decline is the same as above for the total population, however under no scenario does the survey possess enough power ( $\geq 0.9$ ) to detect even the largest logistic declines within the individual subpopulations.

For declines in occupancy rather than abundance, the survey shows increased power. The survey can detect a 3-year decline of 40% or more in the total population, and a 70% or more decline in subpopulations A & B. As with abundance, the differences between a logistic and linear decline in occupancy are minimal when considering the total population. The use of occupancy increases power slightly when attempting to detect declines within each subpopulation, however the survey is limited to only detecting 90% or greater declines in each of them.

#### *5-year decline*

After five years of monitoring, the power of the current survey to detect declines in abundance of Cape Sable seaside sparrows improves considerably. Linear declines in total abundance of 40% or greater can be detected with 90% power, and for individual subpopulations the minimum detectable linear decline drops to 40% (E) 50% (B) 60% (A),

and 75% (C). Logistic declines are harder to detect with 90% power, but are still detectable above 60% for the large subpopulations.

Converting the data to occupancy did little to improve the power to detect 5-year declines in the total population (from 40% to 30% in a linear decline, no change for a logistic decline) or the individual subpopulations. While converting to occupancy improved the power to detect a decline in subpopulation C (from at least 75% to 70%), the power was reduced in subpopulation E by a much greater amount (from at least 40% to 70%). After 5 years of survey information, only very large declines could be detected in the small subpopulations (<80%); and in at least one subpopulation (F) the survey was not powerful enough not detect any decline in abundance.

#### *10-year decline*

Our results suggest that the current survey possesses enough power to detect moderate declines over the span of 10 years. Results for both linear and logistic declines were identical for abundance and occupancy. The current survey could detect as little as a 20% decline in abundance across the entire population. The minimum detectable declines for individual subpopulations were at least 40% (A, B and E), 50% (D) and 60% (C). Converting our data to occupancy reduced the power of the survey, increasing the detectable percentage of minimum necessary decline by anywhere from 5% (total) to 30% (E). Even after 10 years of survey information, there was not enough power to detect any declines in abundance within subpopulation F. However, converting the survey information to occupancy, allows detection of 60% or more declines in this subpopulation.

<Figure 5 about here>

<Figure 6 about here>



## DISCUSSION

Our results indicate that the current Cape Sable seaside sparrow survey is highly zero-inflated, and that a portion of this inflation is due to imperfect detection. Furthermore, our results suggest that this previously un-modeled variation due to excess zeroes is best explained by subpopulation, which implies a spatial rather than temporal cause. We interpret this to imply that detection probability is density dependent, such that sparrow are much harder to detect when present if local density is low. By modeling this variation inherent in the empirical data, we were able to simulate realistic population declines in order to test the power of the current survey. Our use of zero-inflated Poisson model has provided insight into a recurring issue in the published literature for this species. Walters et al. (2000) recommended replicate surveys in order to calculate variance about the mean survey counts, as well as to estimate the probability of detection. Pimm et al. (2002) have claimed that the sparrow surveys are Poisson distributed, and by accepting this assumption, the Poisson standard error is simply the square root of the mean. We agree here with Walters et al. (2002) that it is indeed important to conduct replicate surveys, both because the data violates the assumptions of the Poisson distribution (more zeroes than expected), and because the probability of detection appears not to be constant across all subpopulations. Therefore, by accepting the Poisson assumption, any use of these data to make inference about actual population sizes will be flawed, at least, and misleading at most.

Our power analysis shows that the current survey cannot detect biologically meaningful declines over the short-term (3 years). While occupancy appears to improve survey power over this period, neither occupancy nor abundance allows for detecting

declines to near extinction within individual subpopulations. Although this may seem alarming, a three-year decline is the minimal amount of time necessary to create a trend. Unless the variance about the estimate of abundance or occupancy is extremely low, we should thus expect difficulty in detecting a significant trend in either metric over a 3-year span. Nevertheless, our results suggest there is no value in utilizing the existing survey information as a rapid feedback mechanism for evaluating the effects of Everglades restoration actions on Cape Sable seaside sparrows.

A more promising use of the existing survey is as a tool to evaluate impacts on sparrow population numbers over a five-year window. Power to detect change in occupancy and abundance increase by nearly twice as much over the power associated with a 3-year decline. Even so, our results indicate that the survey can only detect a 40-60% drop in abundance or occupancy over 5 years across the total population, and within the large subpopulations. The power to detect change in the small subpopulations remains very low, showing the ability to detect only very large declines of  $> 90\%$  in most subpopulations or lacking the power to detect even a decline to extinction in one subpopulation. Given that restoration projects tend to focus on only small parts of the whole ecosystem, and thus effect just one or two sparrow subpopulations, the existing survey provides little useful feedback on the fate of individual subpopulations over this time frame.

The existing survey can detect relatively small declines in abundance and occupancy over a 10-year span. Our results suggest that the current survey can detect even a 20% decline in the total population, and anywhere between a 40% and 60% decline in large and small subpopulations respectively (with the notable exception of subpopulation F). Given the long-term outlook of CERP, a 10-year timeline for feedback may be reasonable for

measuring the cumulative effects of restoration projects. However, this time frame is clearly not sufficient if a more rapid adaptive management feedback system is required.

Our method provides a way for Everglades' managers to weigh the effectiveness of a multiple sparrow survey designs to successfully detect declines of various magnitudes over the cost of continuing these over multiple years. However, it does not provide a way to judge what level of population decline is acceptable. For example, at what percentage decline in occupancy or abundance should management actions be triggered? The Cape Sable seaside sparrow emergency action plan (Slater et al. 2008), suggests that a 75% decline in either abundance or occupancy must be observed before active management actions should be implemented (e.g., initiation of captive breeding programs, translocation of sparrows from one part of the range to another). From this perspective, the existing survey provides enough power to confidently trigger emergency actions after 5-years of monitoring and that this conclusion applies across all but the smallest sparrow subpopulations (i.e. D and F).

A similar question revolves around the minimum population size that Cape Sable seaside sparrow should be allowed to reach before restoration actions are modified, or active management is enacted. Minimum viable populations (MVP) are often cited as the size necessary for a population to persist for a designated period of time, with a predefined level of confidence (Shaffer 1981). While we do not have estimates of MVP for the Cape Sable seaside sparrow, Pimm et al. (2002) projected the minimum historical population size of the sparrow at around 10,000 individuals based on the extent of historical survey results and suitable habitat. Brook et al. (2006), in a meta-analysis of 1198 species, found that estimates for MVP ranged widely around a median value of 1377 individuals. Possibly more interesting, however, Brook et al. (2006) found factors commonly associated with extinction

risk were not correlated with MVP. This result suggests that internal population dynamics (e.g., Allee effects) rather than external forces (e.g., habitat loss) become important as populations become very small. The current sparrow population estimate is  $\sim 3000$  individuals, which lies above the mean MVP produced by Brook et al. (2006). However, almost all of these individuals are housed within two subpopulations, which together hold an estimated 3184 individuals (Everglades National Park 2007). The remaining subpopulations are thus well below this estimate of MVP, and accordingly Lockwood et al. (2007) provide evidence that sparrows are operating under internal small population dynamics in these areas. Ensuring that these subpopulations do not continue to decline may be seen as a priority, in which case the existing survey is largely incapable of providing meaningful feedback on the effects of proposed recovery actions.

Finally, adaptive management is dependent on feedback from the system being managed (Gunderson and Light 2007; Holling 1978). We have demonstrated that long-term datasets can be used to estimate the power of data to provide such feedback. Without an understanding of such power, though, managers risk missing critical impacts in enough time to adapt and correct. Additionally, this type of analysis allows managers to assess the relative importance of the variables influencing power. It is possible that by simply increasing the number of survey points, we could increase the power to detect even short-term declines. Alternatively, it is possible that by including a subset of replicate surveys within the season, we could reduce the sample variance enough to significantly improve our statistical power. Ultimately the success of any restoration plan relies on the development of a strong adaptive management protocols. Such protocols must include clear objectives for identifying impacts of projects to the populations of the species of concern. Our work has provided one tool with

which managers can evaluate the strength of monitoring protocols to detect declines in occupancy and abundance.

## **ACKNOWLEDGEMENTS**

This research was generously supported by the US Department of the Interior, Critical Ecosystem Studies Initiative. We would like to thank all of the researchers who have risked their lives flying around Everglades National Park in order to collect these data. Specifically we must acknowledge O. L. Bass Jr., M. Alvarado, L. Oberhoffer, J. Osborne, and S. L. Pimm. Additionally, we would like to thank the many helicopter pilots over the last 16 years who have kept us all safe during our fieldwork. Thanks also to G. Shriver, D. Ehrenfeld, and P.J. Morin for their review of this manuscript, and E. Green for statistical guidance.

## APPENDIX

Because the range-wide helicopter survey lacks within-year replication, direct estimation of detection probability from this dataset is impossible. Therefore, we employed two methods to estimate detection probability for both large and small subpopulations. For the large subpopulations, we used a space-for-time substitution with helicopter survey data from subpopulation B to estimate detection probability. For the small subpopulations, we collected within-season replicate data during 2007 within subpopulation C. Here we describe each method and the results of our analysis.(Maxwell and Jennings 2005)

### *Large subpopulations*

Because subpopulation B has been large stable in occupancy since 1996 (Cassey et al. 1997), we selected all years between 1996 and 2007 for our analysis. Each year, then, was treated as an individual within-year replicate survey (Mackenzie et al. 2005). Because not all points are surveyed in every year, we chose to follow Cassey et al. (2007) and included only the points which had been surveyed 6 or more times between 1996 and 2007. This resulted in 13 replicates (years) for 147 sites across the subpopulation. We used Program PRESENCE (Hines 2006) to estimate detection probability for subpopulation B. We compared two possible models, the first with constant detection over time, and the second allowing detection to vary by survey occasion.

The results from our analysis support a constant detection probability across replicates (model 1). This model had the lowest AIC value, with an AIC weight of 85% (Table A.1). Our results indicate that subpopulation B exhibits a detection probability of 0.57, which means that given a sparrow is present, we would expect to detect it ~60% of the time, on average, across the spatial extent of the subpopulation.

*Small subpopulations*

In 2007, during a demographic study in the small subpopulations (2007), we conducted five replicate point count surveys at 15 survey points within subpopulation C. The survey protocols were identical to those of the range-wide helicopter survey. We used Program PRESENCE to calculate the probability of detection from these data. As before in subpopulation B, we compared two possible models of constant or variable detection over time. The model with constant detection exhibited the lowest AIC score, with an AIC weight of 95% (Table A.2.). The estimate of detection probability was 0.40, 20% less than that of the large subpopulations.



## LIST OF TABLES

Table 1. The relationship between statistical power and associated errors of omission (type II) and commission (type I). The question mark is a reminder of the uncertainty always inherent in hypothesis testing. After Mapstone (1995)

Decision	Reality	
	H <sub>0</sub> true (no decline in sparrows)	H <sub>0</sub> false (decline in sparrows?)
Reject H <sub>0</sub> (decline in sparrows?)	Type I error ( $\alpha$ )	No error - statistical power (1- $\beta$ )
Not reject H <sub>0</sub> (no decline in sparrows)	No error (1- $\alpha$ )	Type II error ( $\beta$ )

Table 2. Parameter estimates for each subpopulation from the best-fit zero-inflated Poisson model ( $\lambda_{2007}$ ,  $\theta_{ZIP}$ ), the logistic regression ( $\psi$ ), as well as our heuristic estimates of zero inflation ( $\theta_{ZIB}$ ) for site occupancy. Lambda values are for the year 2007, which allows for simulating population declines into the future. Estimates are used to simulate population estimates of abundance and occupancy over various scenarios of population decline.

Subpopulation	$\lambda_{2007}$	$\theta_{ZIP}$	$\psi$	$\theta_{ZIB}$
A	0.96	0.92	0.60	0.6
B	1.81	0.48	0.70	0.4
C	0.73	0.84	0.67	0.6
D	0.60	0.92	0.61	0.6
E	1.55	0.63	0.61	0.4
F	0.13	0.79	0.62	0.6

Table 3. Results of fitting 16 years of sparrow survey count data to a series of zero-inflated Poisson models with year and subpopulation as regressors for the number of sparrows counted, and for zero-inflation.

Model	df	AIC	Delta	
			AIC	Weight
$\lambda(\text{year} + \text{subpopulation})\theta(\text{subpopulation})$	13	10643.81	0	0.725
$\lambda(\text{year} + \text{subpopulation})\theta(\text{subpopulation} + \text{year})$	14	10645.7	1.9	0.275
$\lambda(\text{year})\theta(\text{subpopulation})$	8	10754.72	110.91	<0.001
$\lambda(\text{year})\theta(.)$	3	12454.81	1810.5	<0.001

Table A.1. Results from large subpopulation (B) occupancy analysis to derive estimates of detection probability. Data are from 147 sites surveyed at least six times each between 1996 and 2007. Models with constant detection and survey-specific detection were considered.

Model	AIC	$\Delta$ AIC	AIC Weight	Model Likelihood	# Param	-2*LogLike	Detection probability
psi(.)p(.)	2100.04	0	0.85	1	2	2096.04	0.57 (SE=0.01)
psi(.)p(survey)	2103.52	3.48	0.15	0.1755	14	2075.52	0.64 – 0.46 (SE=0.04)

Table A.2. Results from small subpopulation (C) occupancy analysis to derive estimates of detection probability. Data are from 15 sites surveyed five times in 2007. Models with constant detection and survey-specific detection were considered.

Model	AIC	$\Delta$ AIC	AIC Weight	Model Likelihood	# Param	-2*LogLike	Detection probability
psi(.)p(.)	67.13	0	0.95	1	2	63.13	0.399 (SE=0.1)
psi(.)p(survey)	73.09	5.96	0.05	0.05	6	61.09	0.31 – 0.62 (SE=0.2)

## FIGURE LEGEND

Figure 1. Map of Cape Sable seaside sparrow habitat in Everglades National Park, Florida USA. Subpopulations are labeled A-F. The “large” populations are B and E, while the “small” populations are A, C, D, and F.

Figure 2. Histogram of point count values for the total population of the Cape Sable seaside sparrow (1992-2007).

Figure 3. Histograms of point count results for each subpopulation of the Cape Sable seaside sparrow (1992-2007). Subpopulations A, C, D & F are considered “small”, whereas B and E are the only remaining “large” subpopulations.

Figure 4. A schematic of the zero-inflated Poisson simulation. This simplified figure illustrates the idea of a zero-inflated Poisson model consisting of two joint distributions. Essentially, the values generated via the Poisson distribution (using a value for  $\lambda$ ) are multiplied by those generated via the binomial distribution (using a value for  $\theta$ ) to arrive at a final dataset of zero-inflated values.

Figure 5. Power to detect a 3, 5, and 10-year decline in sparrow abundance. Open symbols represent individual subpopulations, while the closed symbol represents the total population. The horizontal line represents the power threshold of 90%.

Figure 6. Power to detect a 3, 5, and 10-year decline in sparrow occupancy. Open symbols represent individual subpopulations, while the close symbol represents the total population. The horizontal line represents the power threshold of 90%.

## LITERATURE CITED

- Boulton, R.L., Lockwood, J.L., Davis, M.J., Pedziwilk, A., Boadway, K.A., Boadway, J.J.T., Okines, D., Pimm, S.L. (2009) Endangered Cape Sable Seaside Sparrow Survival. *J Wildlife Manage* 73: 530-537.
- Brook, B.W., Traill, L.W., Bradshaw, C.J.A. (2006) Minimum viable population sizes and global extinction risk are unrelated. *Ecol Lett* 9: 375-382.
- Bubb, P.J., Butchart, S.H.M., Collen, B., Dublin, H., Kapos, V., Pollock, C., Stuart, S.N., Vié, J.C. (2009) *IUCN Red List Index - Guidance for National and Regional Use*. Gland, Switzerland: IUCN.
- Butchart, S.H.M., Stattersfield, A.J., Bennun, L.A., Shutes, S.M., Akçakaya, H.R., Baillie, J.E.M., Stuart, S.N., Hilton-Taylor, C., Mace, G.M. (2004) Measuring Global Trends in the Status of Biodiversity: Red List Indices for Birds. *PLoS Biol* 2: e383.
- Cade, B., Dong, Q. (2008) A quantile count model of water depth constraints on Cape Sable seaside sparrows. *J Anim Ecol* 77: 47-56.
- Cassey, P., Lockwood, J.L., Fenn, K.H. (2007) Using long-term occupancy information to inform the management of Cape Sable seaside sparrows in the Everglades. *Biol Conserv* 139: 139-149.
- Comprehensive Everglades Restoration Plan (2008) *CERP 2007-2008 Report to the Public*. <http://www.evergladesplan.org>.
- Cohen, J. (1988) Statistical power analysis for the behavioral sciences, 2<sup>nd</sup> edn. New York: Lawrence Erlbaum Associates.

- Curnutt, J.L., Mayer, A.L., Brooks, T.M., Manne, L., Bass, O.L., Fleming, D.M., Nott, M.P., Pimm, S.L. (1998) Population dynamics of the endangered Cape Sable seaside-sparrow. *Anim Conserv* 1: 11-21.
- Davis, S.M., Ogden, J.C. (1994) *Everglades : the ecosystem and its restoration*. Delray Beach, FL: St. Lucie Press.
- Everglades National Park (2007) *Status of the Cape Sable seaside sparrow 2007 survey report*. Homestead, FL. Department of the Interior.
- <http://www.nps.gov/ever/parknews/status-of-cape-sable-seaside-sparrow-2007-survey-report.htm>.
- Gerrodette, T. (1987) A Power Analysis for Detecting Trends. *Ecology* 68: 1364-1372.
- Gunderson, L., Light, S. (2007) Adaptive management and adaptive governance in the everglades ecosystem. *Policy Sci* 39: 323-334.
- Hatch, S.A. (2003) Statistical power for detecting trends with applications to seabird monitoring. *Biol Conserv*.
- Hines, J.E. (2006) *PRESENCE2- Software to estimate patch occupancy and related parameters*. USGS-PWRC. <http://www.mbr.pwrc.usgs.gov/software/presence.html>.
- Holling, C.S. (1978) *Adaptive environmental assessment and management*: 1978.
- IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*. Gland, Switzerland and Cambridge, UK. IUCN Species Survival Commission.
- Jackman, S. (2008) *pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory, Stanford University*. Department of Political Science, Stanford University. R package version 1.03. <http://pscl.stanford.edu/>.



- Jenkins, C.N., Powell, R.D., Bass, O.L., Pimm, S.L. (2003a) Demonstrating the destruction of the habitat of the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*). *Anim Conserv* 6: 29-38.
- Jenkins, C.N., Powell, R.D., Bass, O.L., Pimm, S.L. (2003b) Why sparrow distributions do not match model predictions. *Anim Conserv* 6: 39-46.
- Joseph, L., Field, S., Wilcox, C., Possingham, H. (2006a) Presence-Absence versus Abundance Data for Monitoring Threatened Species. *Conserv Biol* 20: 1679-1687.
- Joseph, L.N., Elkin, C., Martin, T.G., Possingham, H.P. (2009) Modeling abundance using N-mixture models: the importance of considering ecological mechanisms. *Ecol Appl* 19: 631-642.
- Joseph, L.N., Field, S.A., Wilcox, C., Possingham, H.P. (2006b) Presence-absence versus abundance data for monitoring threatened species. *Conserv Biol* 20: 1679-1687.
- Kushlan, J.A., Bass Jr, O.L. (1983) Habitat use and the distribution of the Cape Sable Sparrow. *The Seaside Sparrow: Its biology and management* (TL Quay, JB Funderburg, Jr., DS Lee, EF Potter, and CS Robbins, Eds.). North Carolina Biological Survey Occasional Paper 5: 139–146.
- La Puma, D.A., Cassey, P., Lockwood, J.L. (in prep.) Change in Cape Sable seaside sparrow site use after fire in Everglades National Park, Florida: importance of fire characteristics and time-since-fire.
- Lambert, D. (1992) Zero-inflated Poisson regression, with an application to defects in manufacturing. *Technometrics* 34: 1-14.
- Lockwood, J.L., Boulton, R.L., Baiser, B.H., Davis, M.J., La Puma, D.A. (2007) *Detailed study of Cape Sable seaside sparrow nest success and causes of nest failure.*

- Recovering small subpopulations of the Cape Sable seaside sparrow. A report to the United States Fish and Wildlife Service (South Florida Ecological Services, Vero Beach) and the United States National Park Service (Everglades National Park, Homestead).*
- Lockwood, J.L., Fenn, K.H., Caudill, J.M., Okines, D., Bass, O.L., Duncan, J.R., Pimm, S.L. (2001) The implications of Cape Sable seaside sparrow demography for Everglades restoration. *Anim Conserv* 4: 275-281.
- Lovett-Doust, J., Hegazy, A.K., Hammouda, O., Gomaa, N.H. (2009) Abundance-occupancy relationships and implications for conservation of desert plants in the northwestern Red Sea region. *Community Ecol* 10: 91-98.
- Mackenzie, D.I., Nichols, J.D., Pollock, K.H., Royle, J.A., Bailey, L.L., Hines, J.E. (2006) *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*: Academic Press.
- Mackenzie, D.I., Nichols, J.D., Sutton, N., Kawanishi, K., Bailey, L.L. (2005) Improving Inferences in Population Studies of Rare Species That Are Detected Imperfectly. *Ecology* 86: 1101-1113.
- Mapstone, B.D. (1995) Scalable Decision Rules for Environmental Impact Studies: Effect Size, Type I, and Type II Errors. *Ecol Appl* 5: 401-410.
- Maxwell, D., Jennings, S. (2005) *Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish*, In *J Appl Ecol*. pp. 25-37.
- Nichols, J.D. (2001) Using models in the conduct of science and management of natural resources, In *Modeling in natural resource management: development, interpretation,*

- and application*. eds T.M. Shenk, A.B. Franklin, pp. 11-34. Washington, DC: Island Press.
- Nott, M.P., Bass, O.L., Fleming, D.M., Killeffer, S.E., Fraley, N., Manne, L., Curnutt, J.L., Brooks, T.M., Powell, R., Pimm, S.L. (1998) Water levels, rapid vegetational changes, and the endangered Cape Sable seaside-sparrow. *Anim Conserv* 1: 23-32.
- Pimm, S.L. (1991) The balance of nature?: ecological issues in the conservation of species and communities. University of Chicago Press.
- Pimm, S.L., Lockwood, J.L., Jenkins, C.N., Curnutt, J.L., Nott, M.P., Powell, R.D., Oron L. Bass, J. (2002) *Sparrow in the grass: a report on the first ten years of research on the Cape Sable Seaside Sparrow (Ammodramus maritimus mirabilis)*. Report to the National Park Service.
- R Development Core Team (2009) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. ISBN 3-900051-07-0. <http://www.R-project.org>.
- Recover (2008) CERP Adaptive Management Guidance Manual version 2.1 (DRAFT). 1-204.
- Romesburg, H.C. (1981) Wildlife science: gaining reliable knowledge. *J Wildlife Manag*: 293-313.
- Royle, J.A., Nichols, J.D. (2003) Estimating Abundance from Repeated Presence-Absence Data or Point Counts. *Ecology* 84: 777-790.
- Royle, J.A., Nichols, J.D., Kery, M. (2005) Modelling occurrence and abundance of species when detection is imperfect. *Oikos* 110: 353-359.

- Seavy, N., Reynolds, M. (2007) Is statistical power to detect trends a good assessment of population monitoring? *Biol Conserv* 140: 187-191.
- Shaffer, M.L. (1981) Minimum population sizes for species conservation. *Biosci*: 131-134.
- Sims, M., Bjorkland, R., Mason, P., Crowder, L.B. (2008a) Statistical power and sea turtle nesting beach surveys: How long and when? *Biol Conserv* 141: 2921-2931.
- Sims, M., Bjorkland, R., Mason, P., Crowder, L.B. (2008b) *Statistical power and sea turtle nesting beach surveys: How long and when?*, In *Biol Conserv*. pp. 2921-2931.
- Sims, M., Wanless, S., Harris, M., Mitchell, P., Elston, D. (2006) Evaluating the power of monitoring plot designs for detecting long-term trends in the numbers of common guillemots. *J Appl Ecol* 43: 537-546.
- Sklar, F.H., Fitz, H.C., Wu, Y., Van Zee, R., Mcvov, C. (2001) The design of ecological landscape models for Everglades restoration. *Ecol Econ* 37: 379-401.
- Steidl, R.J., Hayes, J.P., Schaubert, E. (1997) Statistical power analysis in wildlife research. *J Wildlife Manag*: 270-279.
- United States Fish and Wildlife Service (1999) *Multi-Species Recovery Plan for South Florida - The Cape Sable Seaside Sparrow*
- Walters, J.R., Beissinger, S.R., Fitzpatrick, J.W., Greenberg, R., Nichols, J.D., Pulliam, H.R., Winkler, D.W. (2000) The AOU Conservation Committee review of the biology, status, and management of Cape Sable Seaside Sparrows: Final report. *Auk* 117: 1093-1114.
- Welsh, A.H., Cunningham, R.B., Donnelly, C.F., Lindenmayer, D.B. (1996) Modelling the abundance of rare species: Statistical models for counts with extra zeros. *Ecol Model* 88: 297-308.

- Williams, B.K., Nichols, J.D., Conroy, M.J. (2002) *Anal Management of Animal Populations*. San Diego: Academic Press.
- Yoccoz, N.G., Nichols, J.D., Boulinier, T. (2001) Monitoring of biological diversity in space and time. *Trends Ecol Evol* 16: 446-453.
- Zar, J.H. (1998) *Biostatistical analysis*, 4th edn. Upper Saddle River, N.J.: Prentice Hall.
- Zeileis, A., Kleiber, C., Jackman, S. (2008) *Regression Models for Count Data in R*. Journal of Statistical Software. <http://www.jstatsoft.org/v27/i08/>.

## LIST OF FIGURES

Figure 1.

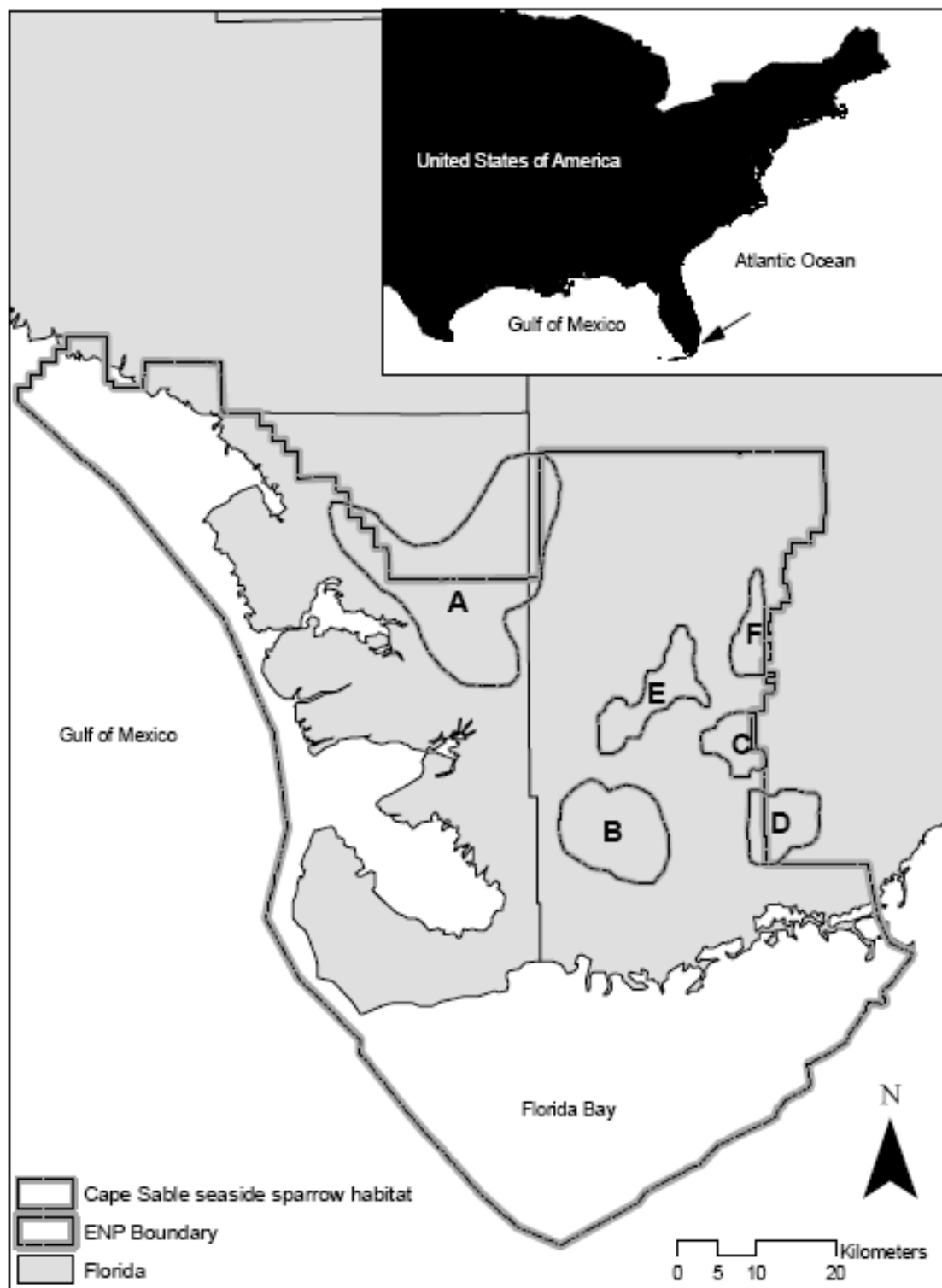


Figure 2.

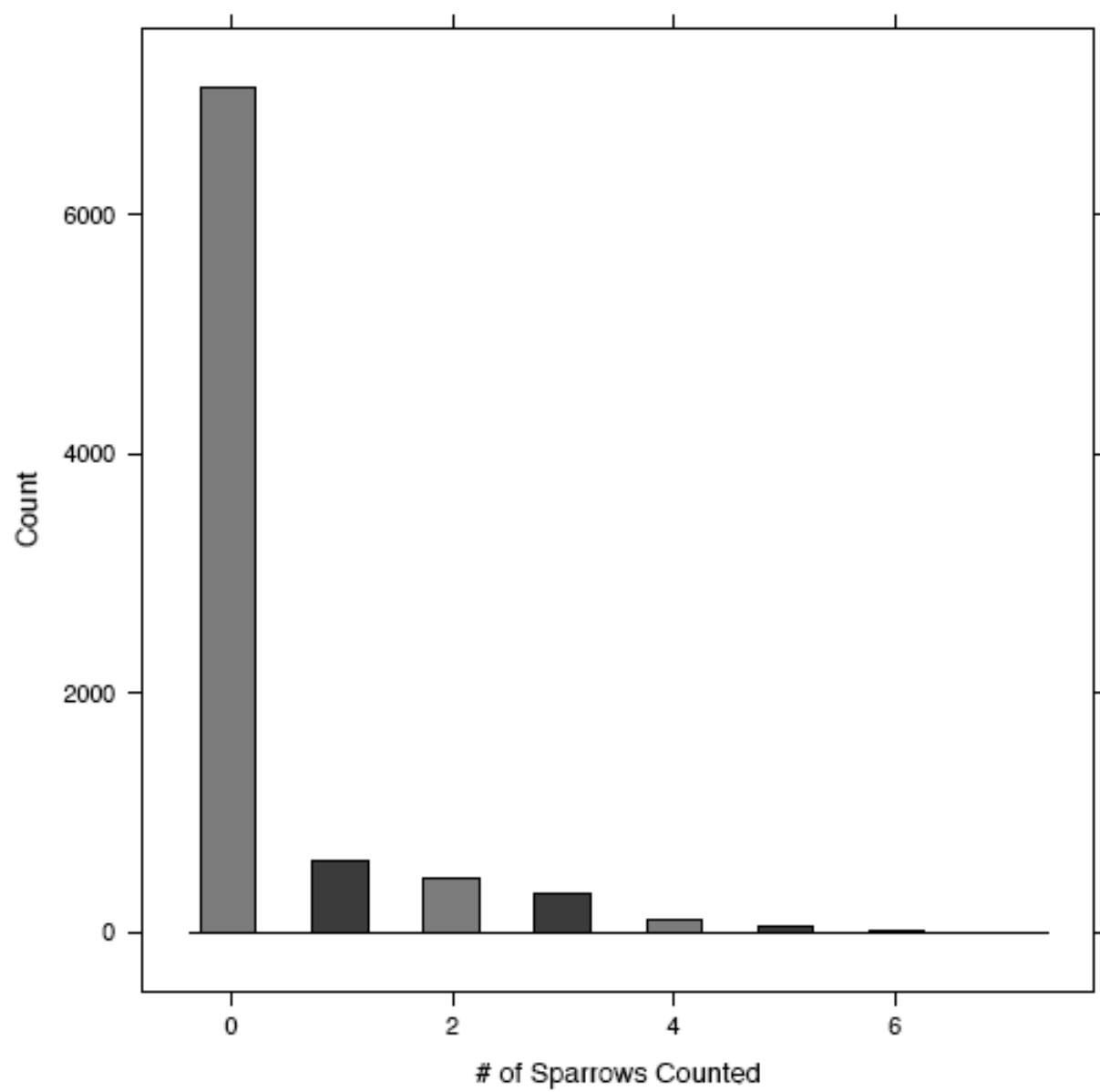


Figure 3.

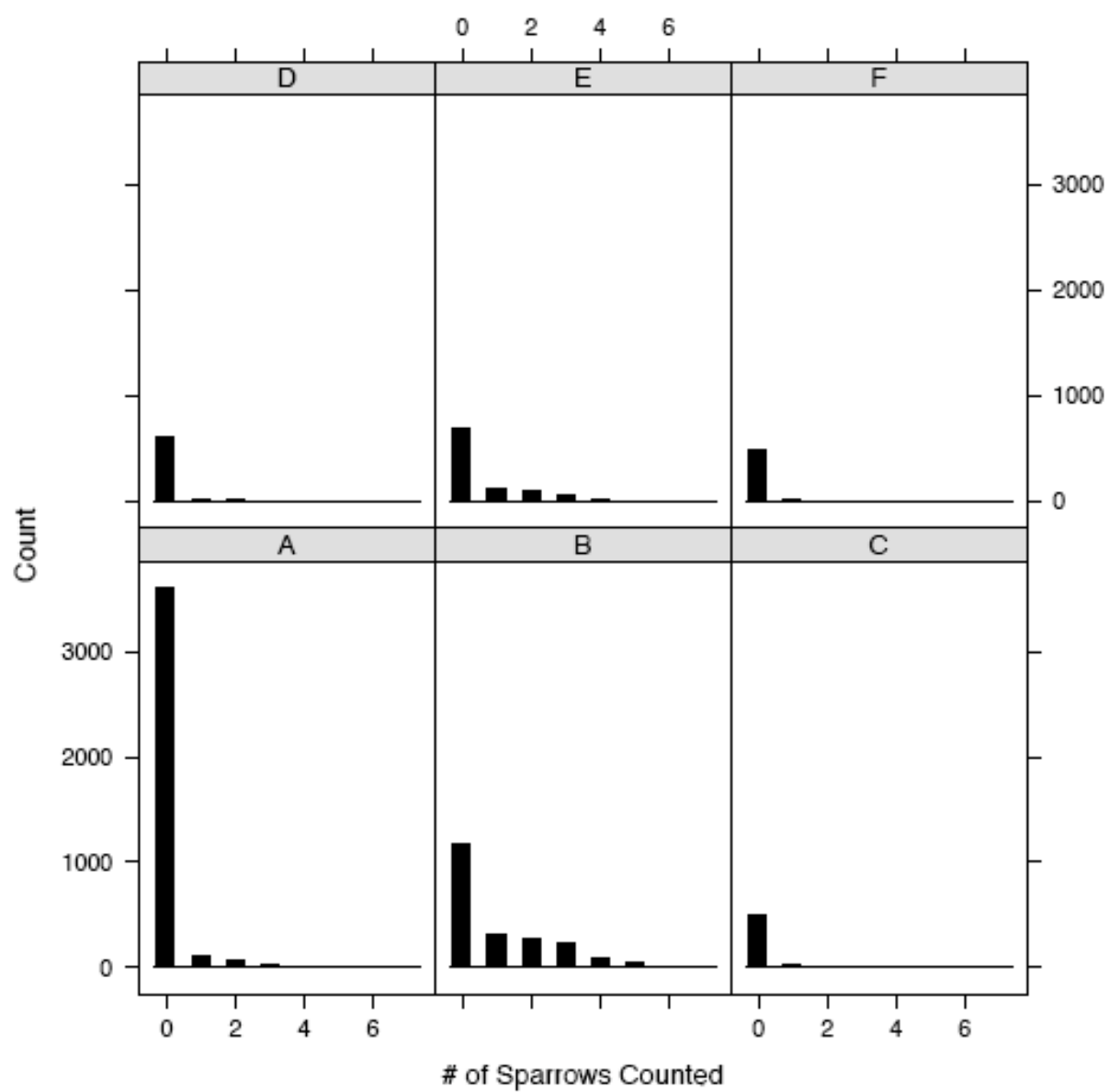




Figure 4.

$$\begin{array}{ccc}
 \text{Poisson } (\lambda) & & \text{Binomial } (\theta) \\
 \left[ \begin{array}{ccc} 5 & 1 & 0 \\ 1 & 2 & 1 \\ 1 & 0 & 3 \\ 1 & 1 & 0 \end{array} \right] & \times & \left[ \begin{array}{ccc} 1 & 1 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 1 \\ 0 & 1 & 0 \end{array} \right] = \left[ \begin{array}{ccc} 5 & 1 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 3 \\ 0 & 1 & 0 \end{array} \right] \\
 & & \text{Zero-inflated} \\
 & & \text{Poisson (ZIP)}
 \end{array}$$

Figure 5.

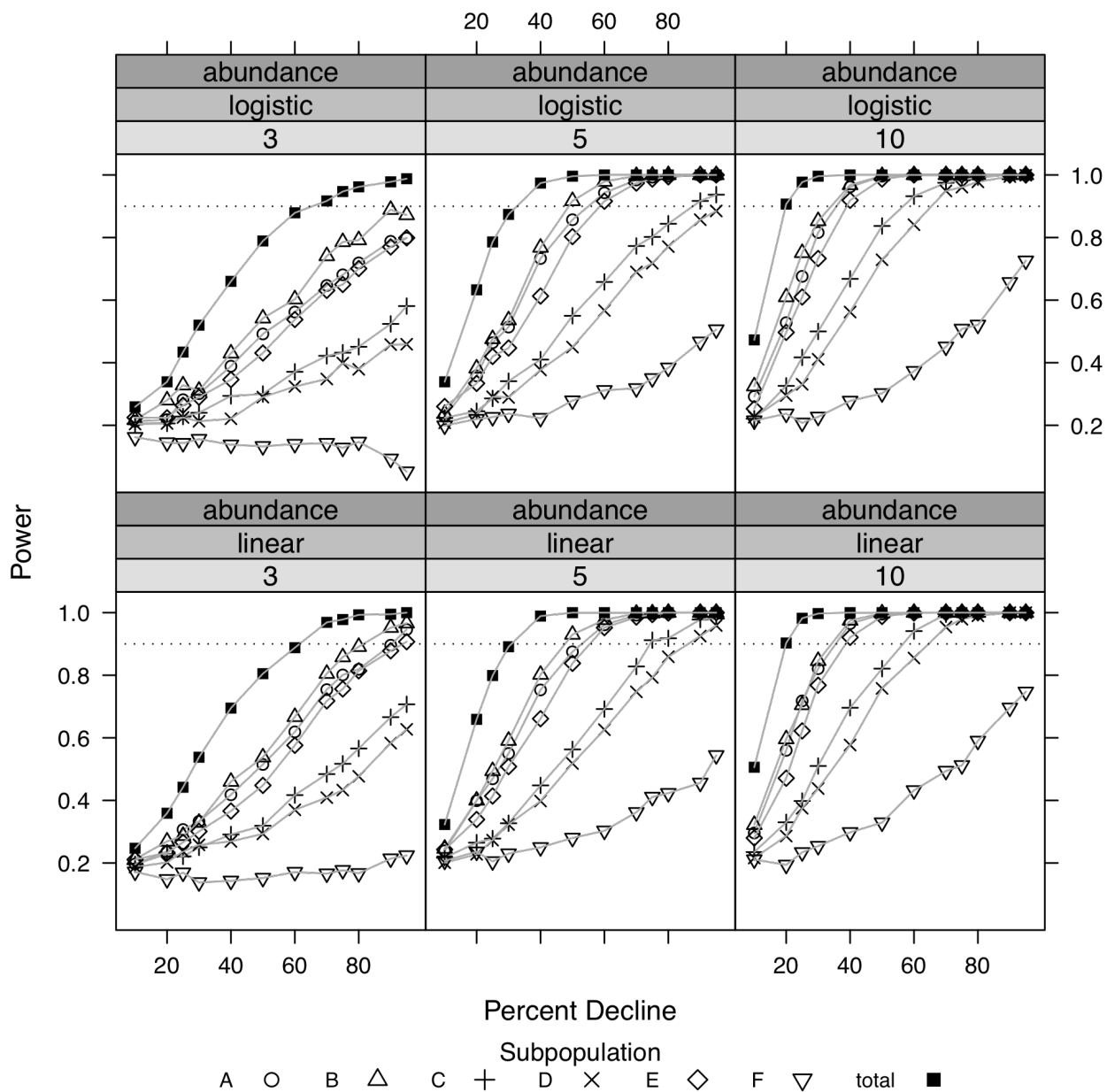
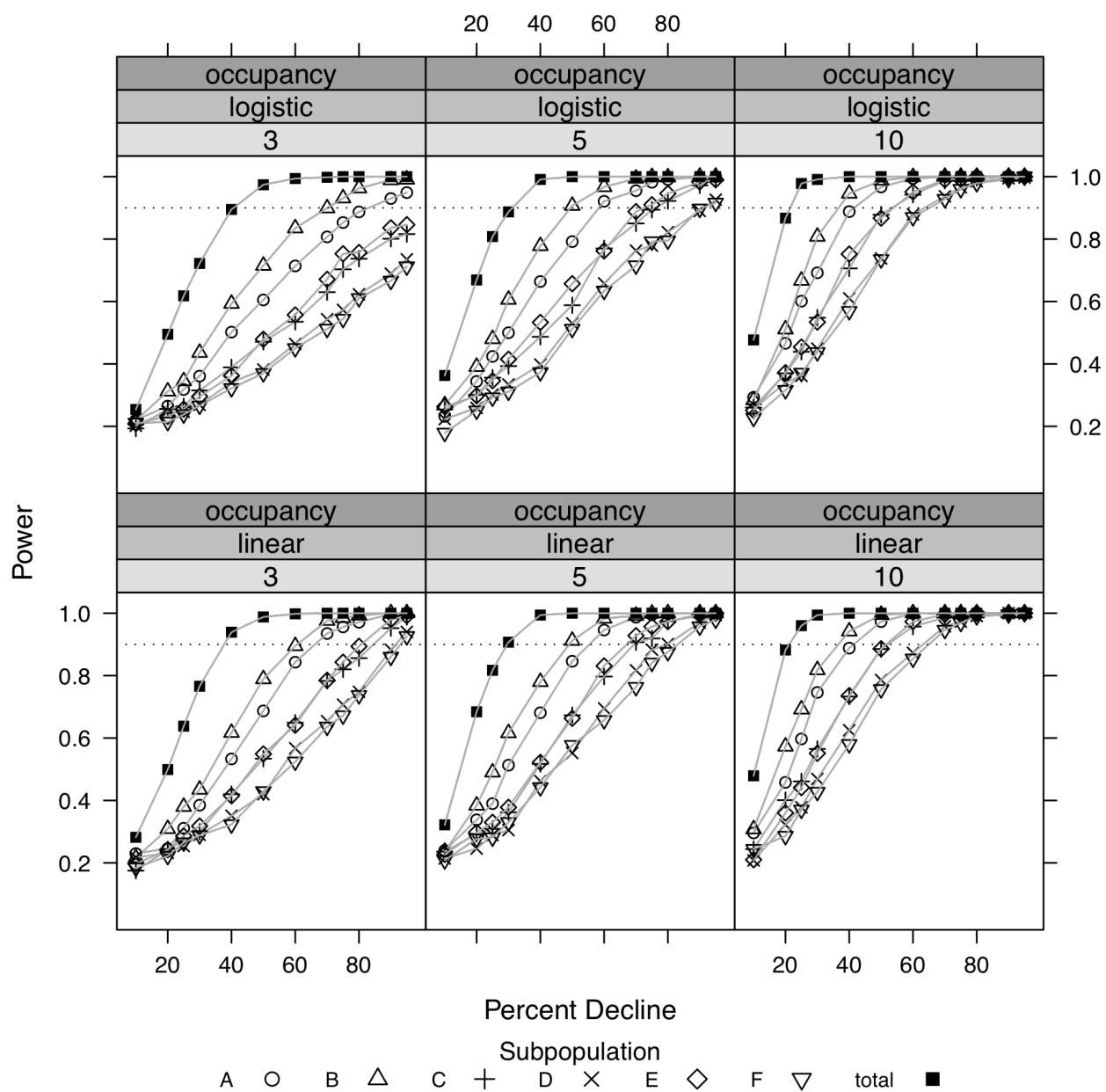


Figure 6.



## CONCLUDING REMARKS

The work presented in my dissertation provides insight into the effects of fire on the Cape Sable seaside sparrow in Everglades National Park, as well as on the statistical power of the current sparrow survey. In this concluding section I present a summary of what my results confirm and refute with regards to our collective understanding of fire effects on the Cape Sable seaside sparrow. With the summary of results, I provide management recommendations that I feel will contribute to the restoration of this ambassador of the Everglades. Finally, I provide recommendations which I feel will improve the current sparrow survey such that it becomes a powerful tool for assessing the response of this species to the changing landscape.

### *Lessons learned from fire*

#### ***Fire negatively affects Cape Sable seaside sparrows in the short term***

This statement is the single most consistent and dominant theme that crosses all research on the effects of fire on sparrows to date. My research supports the work of Werner (1975), Taylor (1983) and Pimm et al. (2002) in documenting that all active sparrow nests are destroyed by fire and that adults appear to perish via the direct effects of fire, or shortly thereafter due to other indirect causes (e.g., predation). In the years after a fire, no one has ever observed a banded adult sparrow that was breeding at a site that had burned. Given that sparrows have an annual survival rate of nearly 70% (Lockwood et al. 2007), the lack of observations of these banded individuals post-fire is remarkable and strongly suggests they did not live long past the fire event.

***Management Recommendation 1: Restrict fire from burning occupied areas of the small subpopulations (C, D, A, and F)***

There is no evidence for habitat senescence thus far that warrants burning the small subpopulations (F, D, C, and A). Subpopulation C is the only one that has shown evidence of recovering its former extent; however, it was accidentally burned in 2007 by an escaped prescribed fire. For a bird with a life expectancy of roughly four years (Lockwood et al. 2007), the chance of individual birds being attuned to fire is unlikely. Werner and Wolfenden (1983) suggested “It seems unlikely that any population that evolved in a fire-maintained environment could be destroyed by that environment, unless the system was altered drastically by man”. Although I agree with this statement, I further state that the tolerance of the sparrow to fire is a population-level response, such that when populations are functional, the reproduction potential of the sparrow is sufficient to replace the individuals killed by periodic fires. Thus the evolutionary adaptation that Werner and Wolfenden write of is in this case only applicable to the sparrows’ ability to produce enough young to replenish the population after catastrophe. Given the small size of these subpopulations and the evidence presented in Lockwood et al. 2007, that breeding success is low in some of these areas, it would only take a small fire to result in the total loss of one of these small subpopulations.

***Management Recommendation 2: Keep dry-season fires out of all sparrow habitat***

As I have shown in Chapter 1 and as reported in Gunderson and Snyder (1994), even under natural conditions, large fires do occur every 10-14 years and these very large fires are especially prevalent at the end of the dry season. Such a fire regime is thus apparently a natural component of the Everglades ecosystem and many species may depend on such

events for their long-term persistence, including possibly the Cape Sable seaside sparrow (although see below). Nevertheless, given that the two largest subpopulations (B and E, which together hold 70% of all occupied sites in any given year; Cassey et al. 2007) are separated by only two kilometers at their closest point, a single large fire could easily encompass both and thus cause the extinction of the sparrow. This scenario is not unlike what happened to the Dusky seaside sparrow just a couple of decades ago (Walters 1992), and is far more likely to happen in the dry-season than in the wet-season. Until the other subpopulations (particularly subpopulations A and C; see below) have recovered 1992 counts, dry-season fires represent a real threat to the persistence of this subspecies.

***Sparrows Are Precluded From Using a Burned Site for At Least Two Years after a Fire***

This statement is supported by the vast majority of research conducted on the effects of fire on sparrows to date, and I have found evidence that this ‘rule of thumb’ holds over the entire range of the subspecies (the only exception being the 1-year recovery observed by Werner 1975). Furthermore, no matter what time of year a fire moves through sparrow habitat, the vegetation in these burned areas will not recover to the extent necessary to support breeding sparrows for at least two years. In some instances, this rate of recovery may be slowed by factors such as depth of the underlying soil, however, evidence for such effects are currently sparse.

***All other things being equal, sparrows will return to burned habitat at densities and nesting success rates equal to unburned habitat by the third year after a fire***

Sparrows will re-colonize burned habitat usually in the third year after a fire. Furthermore, they will return to pre-fire densities and they will enjoy nesting success rates that are typical of the area in which they are breeding. The ‘all other things being equal’ clause in the above statement is critical here. Water flows can alter vegetation to such an extent that sparrows will cease breeding at a site altogether (Pimm et al. 2002), thus if water flows fluctuate while a site is recovering from a fire, it is unlikely that sparrows will return to their pre-fire status. There may be other qualifiers, besides water flow, that will increase the time required for sparrows to return to pre-fire status. One such variable is likely the proportion of habitat burned relative to the size of the subpopulation such that small isolated populations may not recovery as quickly as larger, connected populations. However, we have scant evidence to clarify these relationships even though such information is needed (see below).

***Management Recommendation 3: Develop a new fire management unit for sparrow habitat***

An over-riding concern for the recovery of this subspecies is that we must protect what remaining sparrows currently inhabit the Everglades marl prairies. In order to do so I first recommend treating sparrow habitat as a fire management unit. Currently Everglades Fire Management recognizes several habitat types as having distinctly different natural fire frequencies. The pineland ecosystem, for instance, requires a fire return interval of roughly every four years in order to maintain a healthy over-story of Dade-County Slash Pine (*Pinus elliotii* var. *densa*) and a savannah-like understory of mixed palmettos and forbs. I suggest

that the boundaries of sparrow habitat be delimited based on the best available data from the range-wide helicopter survey, my study, that of Jenkins et al. (2003a, b), and the ongoing vegetation research of Ross et al. (2007). Once delimited, I recommend monitoring of vegetation to determine successional patterns across the range of the sparrow. Based on current knowledge, this time period is in excess of 15 years, and conceivably exceeds multiple decades.

***Management Recommendation 4: Establish fire-effects monitoring plots after all fires that burn within sparrow habitat***

In the event of a fire, a set of plots should be established within and adjacent to the fire and monitored for as long as deemed necessary to determine the sparrow's response. Data on vegetation structure and composition should be collected based on the previous work outlined in Chapter 1, and Ross et al. (2007). Additional information related to the fire such as water depth up to, and following the date of the fire, size of the fire relative to surrounding occupied sparrow habitat, ignition source of the fire, proportion of unburned area within the fire scar relative to the total area burned (a measure of the burn mosaic), and fire severity should be collected and properly archived. The exact details of the data to be collected and how long such data should be collected can be managed and updated at the annual Fire & Sparrow meetings.

***Sparrow habitat may need to burn at 10– to 14–year intervals***



Previous research suggested that sparrow habitat would senesce in the absence of fire, which fits the predominate paradigm for grasslands. However, this evidence was never strongly supported by sound scientific inference. In particular I refute the suggestion stemming from the work of Werner (1975) that sparrow habitat should be burned on a four-year rotation. Instead I find some support for a longer-term process of habitat senescence and suggest that, if a burn rotation is needed at all, it should be on the order of every 10 to 14 years, several years longer than previously suggested by Taylor (1983). Below I suggest that this question deserves far more attention, and that any research program initiated should strive to make very clear mechanistic connections between the effects of *lack of fire* and sparrow habitat use.

***Management Recommendation 5: Burn the sites of Werner's 1975 study***

These sites were areas of deep soils and dense stands of *Muhlenbergia fillipes*. Werner also reported that these sites had small territory sizes and dense packing of individuals, suggesting habitat of high quality. If fire can restore these areas to functional sparrow habitat, and sparrows do reoccupy the area, then we would have our first example of habitat restoration for this species. The sites are easily accessible from Main Park Road, which makes this recommendation logistically feasible. Monitoring protocols that document the recovery of the habitat following such a fire should consider the findings of Taylor (Taylor 1983) when setting an optimization threshold of live and dead biomass.

***Management Recommendation 6: Restore functional sparrow subpopulations across the spatial extent of their range***

While this may be a tall order to present as a management recommendation, it remains the only viable way to allow fire to burn in the ecosystem without the possibility of driving this subspecies extinct. We know that sparrows disperse regularly across subpopulations that are close together (~5 to 10km; Lockwood et al. 2007). We also know that sparrows can recover from large fires as evinced by the recovery of subpopulation B after the Ingraham fire of 1989, and the research in this dissertation. However, we cannot expect sparrows to recover from a fire that burns over nearly all breeding territories in a subpopulation. Specifically I feel strongly that restoring subpopulation A and C would allow a relaxation of the fire restrictions within sparrow habitat. Subpopulation A, if restored, would be buffered by Shark Slough to the east. Subpopulation C would increase the B-C-E subpopulation complex such that sparrows would occupy habitat all the way from western Taylor Slough up to eastern Shark Slough. Should both of these subpopulations be restored, any large-scale fire would (hopefully) leave behind enough sparrow habitat to supply the burned habitat with new recruits once it recovers.

***Unresolved Uncertainty***

Based on all of the available knowledge, I feel confident in my understanding of the initial impact of fire on the Cape Sable seaside sparrow. I also feel confident that once sparrows recover from fire, they may persist for many years in the absence of fire. The current uncertainty lies in the possibility of habitat senescence on the longer end of the time scale, and on whether patches of habitat overlaying deeper soils succeed into sub-optimal habitat relatively quickly as suggested by Werner (Werner 1975). I am also unclear as to the possible

restorative effects of fire in subpopulation A, where hydrology has had a significant negative effect on transforming the vegetation from optimal sparrow habitat to uninhabitable marshland. These questions can be addressed through judicious fire management efforts and a set of statistically powerful monitoring protocols like those suggested in the following section. However, these protocols must be developed within a collaborative framework with Everglades Fire Management, sparrow biologists, and water district officials.

### *Towards a better sparrow survey*

In Chapter 3 I addressed the issue of high variability in the sparrow dataset by using a class of zero-inflated statistical models to make inference about the structure of the data. In doing so, I was able to generate sparrow population data sets exhibiting the same statistical distributions as the real survey data. With these, I simulated population declines of various magnitudes, and tested the statistical power of the current survey to detect such declines. My results indicate that the current survey has very little statistical power to detect declines over short (three years) and moderate (five years) periods. For declines over ten years, my results indicate that the survey can detect moderate declines at the subpopulation level (50-60% drops) and small declines at the total population level (20% or more). From a conservation standpoint, the sparrow survey, in its current form, provides a blunt tool for a job that requires precision.

The need for such

a precise tool has never been greater. As the Comprehensive Everglades Restoration Plan begins to restore water flows to the park, managers require a method for measuring the response of the sparrow to such changes. The simulation code for Chapter 3 is flexible

enough such that park managers can simulate numerous other scenarios they deem important. I hope that Everglades management will use this code to assess alternative measure they can take to improve the statistical inference of the current survey. Below I discuss two possible management actions that would improve the power of the current survey.

***Possible Management Action 1: Increase the total number of survey points***

A straightforward answer to increasing statistical power is to increase the number of points surveyed (i.e. sample size,  $n$ ). Three problems make this option non-viable. First, I chose my sample size based on the number of points known to have held sparrows over the period of record and we know that, at many of these points, sparrows are rarely detected by the survey. Increasing the number of sampling points is thus likely to add survey locations where no sparrows will be detected, and thus this new information will simply increase the variance about the mean. As an example, I simulated a 40% decline (both linear and logistic) over five years while increasing the number of survey points for each subpopulation to the maximum number of points ever surveyed over the period of record (Table C.1).

Table C.1. The number of survey points used, per subpopulation, for the maximum simulation. The numbers used in the original simulations for Chapter 3 are listed for comparison.

<b>Subpopulation -&gt;</b>	<b>A</b>	<b>B</b>	<b>C</b>	<b>D</b>	<b>E</b>	<b>F</b>
Maximum	434	159	43	68	97	39
Original Simulations	75	144	36	28	73	25

The power analysis resulted in a slight improvement in subpopulation A only (from an average power of 0.69 to 0.99). The increase in statistical power is also misleading, since we know that very few birds actually exist in subpopulation A, so the addition of more survey points would not yield more detections in reality.

The second problem with increasing the number of survey points is the cost of the survey. The survey is expensive since all points must be reached via helicopter and multiple observers must be paid for each day of the survey. On average, the survey costs \$400 per survey point. Thus, increasing sample size will be expensive with little return of added power.

Finally, the existing survey covers the entire range for this subspecies and takes nearly 2-months to complete. The sparrow's breeding season peaks during these two months and then individuals become less active and thus less likely to be detected if present. Increasing sample size will increase the time that the survey requires for completion, and any change in underlying detection probability over the span of the survey will also increase variance around estimates of abundance or occupancy.

***Possible Management Action 2: Reduce sample variance by replicating surveys***

Sample variance is the one major component that could potentially be manipulated in order to improve the power of the survey. While my approach considers the existing sample variance, this is seen as the lesser of two options. The best option is to collect data that can explain the excess variance, and therefore estimate it directly. I recommend conducting additional replicate surveys from which park biologists can directly estimate the within-site variance, as well as calculate the probability of detection. This should be carried out across the range of sparrow densities and include samples from each subpopulation. My results, as well as those from Julie Lockwood's work in the small populations, support this relationship between detection probability and sparrow density. Replicate surveys would not need to include the entire helicopter survey, but rather could be a subset of the survey as long as a range of known densities were sampled.

***A final thought***

Lastly, future monitoring of the sparrow should be driven by *a priori* hypotheses. These should take the form of alternate competing models with covariates deemed important to understanding sparrow abundance and detection. This approach is the basic design of active adaptive management, which logistically is the only approach that allows for learning about the ecosystem and the sparrow as we move forward with restoration actions. The reasons for doing so are non-trivial, for as I mention in the introduction, monitoring without clear objectives allows only for the testing of *a posteriori* hypotheses, which are inherently more difficult to disprove. As a result, much more information is necessary for testing them than would be in the case of a carefully planned *a priori* hypothesis. It is our duty to do

anything within our power to improve our precision with which to detect changes in the sparrow population, such that we can act swiftly and prevent the loss of this majestic bird from its rightful home. It is my sincerest hope that the results I have provided in this document may be used towards that end.

## LITERATURE CITED

- Gunderson, L.H., Snyder, J.R., 1994. Fire patterns in the southern Everglades, In Everglades: the ecosystem and its restoration. eds S.M. Davis, J.C. Ogden, pp. 291-306. St. Lucie Press, Delray Beach, FL.
- Jenkins, C.N., Powell, R.D., Bass, O.L., Pimm, S.L., 2003a. Demonstrating the destruction of the habitat of the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*). Animal Conservation 6, 29-38.
- Jenkins, C.N., Powell, R.D., Bass, O.L., Pimm, S.L., 2003b. Why sparrow distributions do not match model predictions. Animal Conservation 6, 39-46.
- Lockwood, J.L., Boulton, R.L., Baiser, B.H., Davis, M.J., La Puma, D.A., 2007. Detailed study of Cape Sable seaside sparrow nest success and causes of nest failure. Recovering small subpopulations of the Cape Sable seaside sparrow. A report to the United States Fish and Wildlife Service (South Florida Ecological Services, Vero Beach) and the United States National Park Service (Everglades National Park, Homestead).
- Pimm, S.L., Lockwood, J.L., Jenkins, C.N., Curnutt, J.L., Nott, M.P., Powell, R.D., Oron L. Bass, J., 2002. Sparrow in the grass: a report on the first ten years of research on the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). Report to the National Park Service.
- Ross, M.S., Sah, J.P., Ruiz, P.L., Jones, D.T., Cooley, H., Travieso, R., Tobias, F., Snyder, J.R., Hagyard, D., 2007. Effect of Hydrologic Restoration on the Habitat of the Cape Sable Seaside Sparrow-Annual Report of 2005-2006 for Everglades National Park:



- Miami. Fl, Southeast Environmental Research Center, Florida International University 46.
- Taylor, D.L., 1983. Fire Management and the Cape Sable Sparrow, In *The Seaside Sparrow: Its Biology and Management*. eds T.L. Quay, F.J.B. Jr., D. Lee, E.F. Potter, C.S. Robbins, pp. 147 - 152. North Carolina Biological Survey and North Carolina State Museum, North Carolina.
- Walters, M.J., 1992. *A Shadow and a song*. Chelsea Green Publishing, Post Hills.
- Werner, H., 1975. The Biology of the Cape Sable seaside sparrow, In *Report to US Fish and Wildlife Service*. Everglades National Park, Homestead.
- Werner, H.W., Wolfenden, G.E., 1983. The Cape Sable Sparrow: its habitat, habits, and history, In *The Seaside Sparrow, its biology and management*. North Carolina Biological Survey and North Carolina State Museum.

# DAVID LA PUMA

## Education

Institution	Degree	Year
Ithaca College	BA Environmental Studies	1997
Rutgers University	Ph.D. Ecology & Evolution	2010

## Peer-reviewed Publications

**La Puma, D.A.**, Elgersma, K.J., Lockwood, J.L., 2009 (anticipated). Power to detect declines in occupancy and abundance in a rare species: lessons from a long-term dataset **Bird Conservation International**, In Prep.

**La Puma, D.A.**, Cassey, P, Lockwood, J.L., 2009 (anticipated). Change in Cape Sable seaside sparrow site use after fire in Everglades National Park, Florida: importance of fire characteristics and time-since-fire.

**Ecological Applications**, In Prep.

Baiser, B.H., Lockwood, J.L., **La Puma, D.A.**, and Aronson, M.F. A Perfect Storm: Two Ecosystem Engineers Interact to Degrade Deciduous Forests of New Jersey. **Biological Invasions**. 10 (6), 785-795.

**La Puma, D.A.**, Lockwood, J.L., Davis, M.J., 2007. Endangered species management requires a new look at the benefit of fire: The Cape Sable seaside sparrow in the Everglades ecosystem. **Biological Conservation** 136, 398-407.

## Popular science Publications

**La Puma, D.A.** November-December 2009. Endemic in the Everglades **WildBird Magazine** In Prep.

**La Puma, D.A.** July-August 2007. Mega-Scale Observations: Use weather radar to predict birding conditions in your neck of the woods. **WildBird Magazine** 21 (4), 34-39.

## Reports

2007 Lockwood, J.L., **La Puma, D.A.**, Cassey, P., Davis, M.J., and Fenn, K.H. Final Report: Fire effects on Cape Sable seaside sparrow Demography. Everglades National Park, Homestead, Florida.

2007 Lockwood, J.L., Boulton, R.L., Baiser, B.H., Davis, M.J., and **La Puma, D.A.** Detailed study of Cape Sable seaside sparrow nest success and causes of nest failure. Recovering small populations of the Cape Sable seaside sparrow. US Fish and Wildlife Service, Vero Beach, Florida.

2006 Lockwood, J.L., **La Puma, D.A.**, Cassey, P., Davis, M.J., Fenn, K.H. Effects of fire on the Cape Sable seaside sparrow 2006 Annual Report. US National Park Service, Homestead, Florida.

2004 Lockwood, J.L. and **La Puma, D.A.**, Fire effects on Cape Sable seaside sparrow demography: 2004 final report. US Fish and Wildlife Service, Vero Beach, Florida.

## Current Research

**PhD Dissertation**, Effects of fire on the Cape Sable seaside sparrow: Adaptive management planning for the future state of a restored Everglades ecosystem, January 2004 - Present

Tested the direct effect of fire on the demography and habitat structure and composition of the federally endangered Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) in Everglades National Park

Identified the mechanistic link between fire and recolonization of burned habitat by sparrows (La Puma et al. 2007)

Employed occupancy modeling to scale our results to the landscape level and determined the pattern of sparrow return time after fire (La Puma et al, In Prep)

Conducted a sensitivity and feasibility analysis of three survey methods to aid management in detecting changes to sparrow abundance and occupancy (La Puma, In Prep)

**Principal Investigator** (in collaboration with Inga La Puma and Benjamin Baiser), Avian diversity and distribution across a successional gradient at the Hutcheson Memorial Forest, Somerset, NJ. July 2006 – Present

**Co-Principal Investigator** (in collaboration with Benjamin Baiser (PI)), Spatial distribution of breeding birds within the Old Growth Hutcheson Memorial Forest, Somerset, NJ. July 2007 – Present

**Principal Investigator**, Using Doppler Radar to predict migrant landbird concentrations in New Jersey and Florida, January 2004 – Present