

WADING BIRD (CICONIIFORMES) RESPONSE TO FIRE
AND THE EFFECTS OF FIRE IN THE EVERGLADES

By

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To all those with inquiring minds

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Abstract of Dissertation Presented to the Graduate School
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WADING BIRD (CICONIIFORMES) RESPONSE TO FIRE
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Despite considerable knowledge about fire effects on wildlife in uplands, there is a relative paucity of information about fire effects on wetland-dependent wildlife. Many wetland communities are pyrogenic, and even those that rarely experience wildfire naturally are often burned with prescribed fires. Fire in wetlands was initially conducted for the purpose of benefiting waterfowl and muskrat. Since then, there is recognition that other species such as sparrows, wading birds, and salamanders are affected by fire, at least on a short-term basis.

Wading birds may benefit from fire through the exposure of prey after vegetation removal, or through a trophic response to added nutrients and light resulting from fire. I determined whether wading birds select for and benefit by foraging in burned areas in the central Everglades. Great egrets and white ibis selected for burned ridges and adjacent sloughs and avoided areas of dense, tall, unburned sawgrass. Great egrets had higher capture rates in sloughs adjacent to burns than in burns, but were more efficient at capturing prey in burned areas than in the adjacent sloughs. Prescribed fires created short-term shallow water habitats with limited submerged and emergent vegetation, apparently making prey more accessible.

Fire releases nutrients and increases light via the combustion of vegetation. I manipulated light and nutrients in a 2x2 factorial experiment to determine fire effects on primary production and standing stock of fish in the oligotrophic wetlands of the Everglades. I used prescribed burns (nutrients) and mowing with removal of vegetation (no nutrients) to manipulate nutrients. To manipulate light, I constructed shade houses (no light) to limit light and left other plots open (light). Significantly greater periphyton cover and mass (dry weight) per area was observed in the Nutrients + Light treatment than in other treatments. Fish generally did not respond to treatments, but least killifish (*Heterandria formosa*) had larger individuals while flagfish (*Jordanella floridae*) and sailfin mollies (*Poecilia latipinna*) had smaller individuals in nutrient treatments. Increases in size may equate to increased reproductive output or to differences in age structure of fish using these areas. Fire apparently augments primary production, however fish response was limited.

CHAPTER 1 INTRODUCTION

Fire is a natural process in many wetlands that helps maintain the structure, function, and communities of these wetlands (DeBano et al. 1998). Fire return intervals of wetlands range from approximately once per year to once every 300+ years, depending on the hydrological cycle, vegetative growth, and other environmental factors. Fire typically resets succession in wetlands, maintaining species associations typical for the wetland. Our knowledge of the effects of fire on wetland-dependent wildlife is limited in scope. In this dissertation, I report three studies aimed to improve our knowledge of fire effects on foraging ecology of wading birds. These studies include a literature review that identifies existing knowledge of effects of fires on wildlife in wetlands (Chapter 2), an observational study on wading bird foraging in burned areas that addresses benefits of foraging in burned areas (Chapter 3), and an experimental manipulation of burned habitats to fire effects on wading bird prey (Chapter 4).

Much of the early literature of fire effects on wildlife is observational in nature due to the lack of control treatments and replication (e.g., Lynch 1941, Givens 1962, Zontek 1966). Most fire effects “studies” are reports related to using fire to manage wetlands for waterfowl production. Since the mid-1990s, a need to understand the effects fire has on target and non-target species has resulted in many more studies of fire effects on wildlife in wetlands. In spite of this trend, studies on the effects of fire on wildlife are still very limited (Chapter 2). I review the available literature of fire effects on wetland-dependent wildlife to illustrate how fire in wetlands impacts wildlife in comparison to fire in uplands.

Wading bird selection of foraging areas is driven largely by water depth, prey availability, and vegetation density (Bancroft et al. 2002, Gawlik 2002, Lantz et al. 2010, Pierce and Gawlik 2010, Lantz et al. 2011). Changes in any of these affect foraging success of wading birds. Anecdotal observations by fire management specialists and scientists of wading birds (Order Ciconiiformes) foraging in burned areas suggest that these birds may benefit from burns. Fire removes vegetation (exposing additional areas containing prey resources), releases nutrients and increases light, and changes foraging habitat, potentially attracting wading birds. I generated four hypotheses to test whether wading birds preferred foraging in burns and if they benefited by foraging in these burned areas (Chapter 3). I hypothesized that wading birds would select for burned areas more than unburned areas (H_1 ; Fig. 1-1). I hypothesized that fires make prey available by injuring or killing prey during the burn (H_2). I also hypothesized that prey densities would be greater in burned than unburned sawgrass because of increased primary production post-burn resulting from light and nutrients (H_3). Finally, I hypothesized that wading birds would have a higher capture rate (captures per minute) and capture efficiency (captures per attempt) in burned areas than in unburned areas (H_4).

Fire effects on the aquatic community in wetlands are relatively unknown. Increases in nutrients and light stimulate primary production (Mosisch et al. 2001) and provide additional food resources to primary consumers. If aquatic consumers are food-limited, increased food resources may lead to an increase in their size, nutritional value, or abundance, any of which could benefit predators such as wading birds. In Chapter 4, I investigate whether the release of nutrients and increase of light to the underlying

substrate by fire increases periphyton primary production with a concordant response by the fish community. I hypothesized that an increase in light and nutrients would result in more periphyton biomass and cover (H_5). I also hypothesized that total and individual fish size, condition factor, and relative abundance would increase, assuming that periphyton biomass increased (H_6). If light and nutrients post-fire do not result in a subsequent increase in periphyton, there is then little evidence to suggest that fire increases primary productivity. Rather, wading birds and other predatory animals may respond to burns because prey are easier to catch or attracted to recently burned areas for reasons other than an increase in primary productivity.

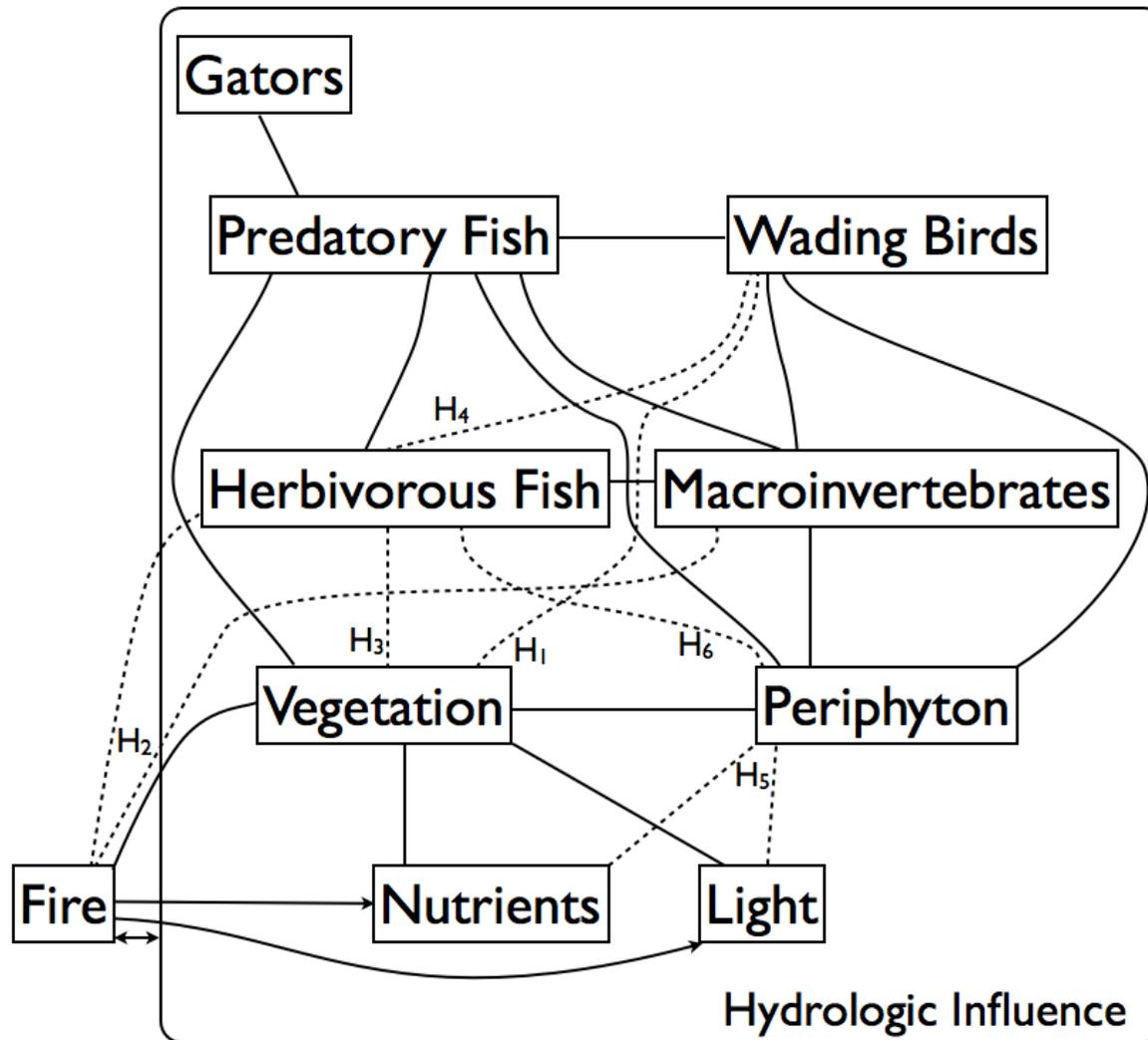


Figure 1-1. Simplified food web model in the Everglades illustrating hypotheses (numbered hypotheses (e.g., H₁) correspond to dashed lines to illustrate pathways) tested in Chapters 3 and 4. Lines with arrows indicate direction of influence. Box indicates the realm of hydrologic influence on this food web.

CHAPTER 2 EFFECTS OF FIRE ON WETLAND-DEPENDENT WILDLIFE: A REVIEW

Introduction

Fire is a natural disturbance in many upland systems that affects nutrient cycling, plant species composition, pest and pathogen prevalence, and wildlife use and movements on the landscape (Whelan 1995). Fire is also a natural disturbance in many wetland systems. Occurrence and frequency of fire can be limited by environmental conditions, with fire often starting during periods of drought or a drop in water levels (DeBano et al. 1998). As in terrestrial systems, fire can affect succession in wetlands (e.g., Wharton et al. 1982, Kantrud et al. 1989, Laderman 1989, Gagnon 2009), resulting in a shift in vegetation composition and maintenance of function in the wetland. Effects of fire are also dependent on the timing of the fire and conditions of the wetland (e.g., water levels). However, our understanding of fire effects on wetland-dependent wildlife is limited and while inferences from upland studies may be drawn, sufficient differences of fire effects between uplands and wetlands exist to warrant further study of fire effects on wetland dependent wildlife.

Fire frequency in wetlands is largely dependent on environmental conditions such as hydrology, unlike terrestrial habitats (Mitsch and Gosselink 2007). Fire frequency is important for sustaining the structure and function in many wetlands. For example, feedbacks between fire and hydrology reinforce the dome shape of isolated cypress domes (Watts et al. 2012). Regular fires maintain wetland structure and dynamics in pyrogenic wetlands such as the Everglades. This wetland experiences a high density of lightning (Orville and Huffines 2001) that ignites wildfires just before the onset of the wet season when water depths are typically at their lowest level (Slocum et al. 2007). The

dominant wetland vegetation grows quickly and senesces, a growth form conducive to spreading frequent fires (Wade et al. 1980). Less frequent fires can also help maintain structure and function of certain wetlands. In northern climates, peatlands and bogs set in forested ecosystems burn on the same infrequent time scale as the surrounding forest (DeBano et al. 1998), helping maintain the wet, anoxic conditions that perpetuate this type of wetland. If fires are too frequent species such as Atlantic white cedars may be eliminated via additional fires post-germination (Laderman 1989).

Prescribed fires in terrestrial systems tend to be conducted outside of the natural fire season, altering the expected effects of fire on the ecosystem (Cox and Widener 2008). This appears true for wetlands also, since prescribed fires are often conducted in winter when lightning is less prevalent (Orville and Huffines 2001). Prescribed fires are designed to burn fuels only above the surface of the water and avoid ignition of the peat soils. Such fires are frequently conducted to create early-succession habitat for wildlife such as muskrat and waterfowl. Caution is taken when planning prescribed fires to minimize damage to nesting waterfowl while increasing food for wildlife (Lynch 1941, Hoffpauir 1961). Thus, prescribed fires can be used to achieve goals that may not be met through letting wildfires burn.

In contrast to prescribed fires, wildfires that occur when water levels drop or during droughts may result in peat fires. Fire in peatlands impacts the vegetative structure, peat depth, and nutrient availability (DeBano et al. 1998). Peat fires typically are impossible to control, but change vegetation composition and provide deep-water habitat which may be important for certain wildlife species such as diving ducks and turtles. However, deep peat fires can also eliminate desired wetland species and alter

vegetation composition (e.g., Atlantic white cedar swamp to deciduous hardwoods; Laderman 1989).

While fire has long been recommended as a management tool in wetlands for waterfowl habitat enhancement and increased food quality for herbivorous species (e.g., Lynch 1941, Givens 1962, Lugo 1995, Nyman and Chabreck 1995), only more recently have studies started to quantify the effects of fire on other avian species and other wetland dependent wildlife (Fig. 2-1). Effects of fire on upland species may partially be used as a guide for what to expect for wetland species. Birds often target prey fleeing the flame front (e.g., Tewes 1984), herbivorous species take advantage of nutritious regrowth and granivores of increased seed or mast production (Lyon et al. 2000), and other species target insects that exploit weakened or killed vegetation (e.g., Warren et al. 1987, Cox and Widener 2008, Hutto 2008). In addition to food resources, changes in habitat structure and cover affect how species utilize wetlands, increasing use for species that prefer open areas or sparse vegetation and decreasing use for species that prefer dense cover. While more work to understand responses to fire by birds and other species in grasslands and forests is still necessary (Warren et al. 1987, Russell et al. 1999, Pilliod et al. 2003, Saab and Powell 2005), our understanding of fire effects on wetland-dependent wildlife lags far behind our knowledge in uplands. Much work is still needed if fire is used to manage wildlife habitat and minimize unintended consequences on species of management concern and non-target wildlife.

The literature of fire effects on wetland-dependent wildlife is fairly limited, recent, and primarily focused on presence/absence and abundance of avian species. While species presence and abundance post-fire is important to determine whether species

respond to fire, understanding the mechanism for the response is much more informative in making decisions regarding the use of fire for the purpose of management of wildlife species and wetland ecosystems. However, few studies have looked at underlying causes to the responses to fire by species studied. Kirby et al. (1988) reviewed fire effects in wetlands, creating an annotated bibliography of peer-reviewed and gray literature publications. For an extensive, although somewhat dated, bibliography of fire effects on wetland systems and effects on wildlife, I recommend readers consult Kirby et al. (1988). Subsequently, Mitchell et al. (2006) thoroughly reviewed the effects of fire and other management strategies in coastal marshes on birds. Russell et al. (1999) and Pilliod et al. (2003) reviewed the herpetofauna literature, illustrating how scant our knowledge is of fire effects on herps in wetlands. Since these reviews, a number of studies have been published that begin to address some of the gaps in our knowledge. While many studies of fire in wetlands investigate the effect of fire on wetland vegetation from which we may be able to draw some conclusions about wildlife response, direct and indirect effects on wildlife are typically not included in these studies, leaving many unanswered questions about wildlife response. In this review, I focus on ecological effects on wildlife of fire. A summary table of studies can be found in Table 2-1.

Mammals

Only a handful of studies of fire effects on mammals in wetlands exist, despite mention of the ease of trapping some furbearing species post-fire and the use of fire in marshes to enhance forage for cattle (e.g., McAtee et al. 1979). I found 8 studies of fire effects on mammals in wetlands, most published between 1940 and 1970 (Fig. 2-1). Fire effects studies from this era typically did not include information indicating

experimental rigor had been applied to observations or management suggestions. Fire typically does not cause mortality of muskrats or deer because they have escape strategies such as taking refuge or fleeing (Lynch 1941). However, fire removes cover, exposing the mammals inhabiting these marshes. Humans often burned marshes so furbearers such as muskrat could be more easily managed and trapped by concentrating them in the limited remaining cover in marshes (Lynch 1941, Singleton 1951, Givens 1962, Perkins 1968, Ward 1968).

Burning vegetative cover in wetlands results in poor habitat for most rodents until vegetation regrows (Tewes 1984). Wetlands in high-altitude areas of Kamborg Nature Reserve, South Africa are burned triennially and represent areas of high small mammal populations and richness, including the preferred habitat of South African vlei rat (*Otomys irroratus*; Bowland and Perrin 1993). Natal Mastomys (*Mastomys natalensis*) was captured in wetlands only after burning, indicating that changes due to fire either exposed or benefited this species, however Bowland and Perrin (1993) did not give reasons for this response. Other small mammal populations initially declined post-burn due to reduced cover and food supply.

Herbivores such as muskrat and deer supposedly benefit from fire due to increased nutritive content and marsh grass production and an increase in preferred food plants, respectively (Lynch 1941, Loveless and Ligas 1959, Smith et al. 1984). Beavers have also long been thought to benefit from fires through regeneration of woody forage, however, spring fires that burn up to the edge of wetlands appear to cause beaver lodge abandonment by reducing habitat quality in Elk Island National Park, Alberta Canada (Hood and Bayley 2003, Hood et al. 2007). A single fire resulted

in abandonment of lodges for multiple years post-burn and additional fires resulted in further lodge abandonment. Interaction of fire with high levels of herbivory and drought further exacerbated reductions in habitat quality (Hood and Bayley 2003, Hood et al. 2007). Thus, frequent fires could significantly reduce beaver populations in this habitat by reducing forage already limited by herbivory, rather than benefiting this species with increases in woody plant regrowth.

Avians

Avians are the longest and most studied group in regards to response to fire in wetlands (Fig. 2-1). I found 33 published studies of fire effects on avians in wetlands, largely on sparrows and waterfowl. While gaps in our knowledge of fire effects on upland species exist (Saab and Powell 2005), we know much less about the effect of fire in wetlands on avians inhabiting these ecosystems. The first reports on the use of fire to manage for wetland species started with waterfowl. Thereafter, effects on other wetland-dependent species were reported. Most studies focus on the effects of changes in vegetation affect presence and abundance of avian species post-burn, yet effects on foraging and nesting are being incorporated into studies.

Direct Mortality Resulting from Fire

Instances of direct mortality due to fire appear to be rare. Typically, wildlife can avoid mortality via fire whether by fleeing or taking refuge in burrows, underwater, or densely vegetated moist areas. However, mortality due to fire does occur. During a wildfire, approximately 50 adult white ibis (*Eudocimus albus*) with fire-charred feathers were found dead in desiccated and brown cattail (Epanchin et al. 2002). Epanchin et al. (2002) suggest scenarios for the death of these birds, including debilitation due to smoke inhalation, taking refuge from the fire in the cattail stand before it burned, or

foraging close to the fire line as smoke and flames corralled and drove prey items. While birds taking refuge in vegetation near a burn may seem counterintuitive when sloughs with open water would be a safer refuge, other birds have similarly been reported to take refuge in a wet area of marsh, resulting in mortality when fire burnt the refugia (Legare et al. 1998).

Use of Vegetation Post-Burn

Waterfowl (Family Anatidae) were some of the first species suggested to benefit from the use of fire to manage vegetation in and around wetlands (Lynch 1941, Givens 1962, Schlichtemeier 1967, Perkins 1968, Ward 1968). Lynch (1941) reported that experimental fall burns in the Chenier Plains along the coast in southwestern Louisiana increased the abundance of snow geese (*Chen caerulescens*) and also attracted Canada (*Branta canadensis*) and white-fronted geese (*Anser albifrons*). This supposedly was the first time snow geese had been seen at Lacassine National Wildlife Refuge in southwestern Louisiana. While Lynch (1941) gave no indication of presence or abundance of these species in unburned areas, abundance of ducks, particularly mallards (*Anas platyrhynchos*) and northern pintails (*A. acuta*), were noted as being in the thousands in the burned areas. Hochbaum et al. (1985) found no difference in waterfowl use of wetlands with burned and unburned edges (within 10 m of wet meadow edge) after spring and fall fires in southern Manitoba and southeastern Saskatchewan, Canada. Waterfowl benefit from changes in vegetative structure if burns are timed appropriately, as discussed in a later section.

Sparrows typically inhabit dense, grassy areas so changes in vegetative cover can be expected to affect sparrow presence and abundance post-burn. After a winter prescribed fire in the Chenier Plains in coastal southwestern Louisiana, most sparrows

(i.e., seaside (*Ammodramus maritimus*), Nelson's sharp-tailed (*A. nelsoni*), and swamp (*Melospiza georgiana*)) did not return to burned areas for at least a year or more (Gabrey et al. 1999). Gabrey and Afton (2004) showed that sparrows are typically at lower abundances during the first breeding season post-burn on plots burned in winter than prior to the burn, but by the second year have returned to pre-burn abundances. When vegetative structure returned to pre-fire levels, sparrows utilized recently burned habitat and in some cases, were found in higher abundances in the second year post-burn than in unburned plots (Gabrey and Afton 2000). In the third year, sparrows per plot remained at abundances similar to year two post-burn, corroborating the importance of dead vegetation structure for sparrows (Gabrey et al. 2001). Similarly, Vogl (1973) found swamp and song (*M. melodia*) sparrows in greater abundance within one year in the unburned part of a pond shoreline in the panhandle of Florida compared to the burned portion. However, no further observations were provided and no knowledge of habitat, foraging resources, long-term use, or behavior were provided. In shrub/scrub wetlands in northern Minnesota, Hanowski et al. (1999) counted more clay-colored (*Spizella pallida*), savannah (*Passerculus sandwichensis*), and Le Conte's (*A. leconteii*) sparrows in managed (i.e., sheared and/or burned) than unmanaged wetlands. Increased abundances of Le Conte's sparrow suggested that sheared and burned treatments (treatment blocks grouped into 0-3 years post-treatment, and 3+ years post-treatment) may benefit this species, but not significantly more than other treatments ($p=0.053$). Based on the yearly changes of sparrow responses in the Chenier Plains, it is likely that categorizing treatments into 3-year time-blocks obscured responses by species.

Wintering sparrows that tend to breed in upland habitats responded differently to fires in wetlands than wetland-dependent sparrows. White-throated sparrows (*Zonotrichia albicollis*) were observed in greater abundance on the burned than unburned shoreline of a pond (Vogl 1973). Henslow's sparrows (*A. henslowii*) wintered at higher densities in Gulf Coast pitcher plant bogs the first year post-burn than in subsequent years post-burn (Tucker and Robinson 2003). Fires during the growing season appeared to attract sparrows for more years, suggesting that growing season burns may benefit sparrows longer. However, forb density and availability of seed stalks drove the occupancy of these bogs by Henslow's sparrows more than season of burn. Fire and season of burn can be used to manipulate availability of food resources.

Wrens in wetlands tended to avoid recent burns while there was little or no vegetation. In coastal marshes in the Chenier Plains, sedge wrens (*Cistothorus platensis*) were not found during the winter in areas burned the previous month, but were present the following winter in approximately an equal number of burned and unburned plots (Gabrey et al. 1999). During the breeding season, Gabrey et al. (2001) found no difference in number of wrens (i.e., marsh (*Cistothorus palustris*) and sedge wrens) per survey among years or treatments in the three years after winter prescribed burns in the Chenier Plains. However, sedge wrens were absent from burned plots the first summer, but were in these plots in subsequent years. Marsh wrens were encountered in burned plots in the first month and again, one year later, after a winter burn, but were more frequently observed in unburned plots in both years. Four months after a late winter burn, sedge wrens (named grass wren in this study) were detected in burned *Juncus* marshes in the Mar Chiquita Biosphere Reserve, Argentina, and after six

months abundances were similar between burned and unburned treatments in *Juncus* marshes (Isacch et al. 2004). Sedge wrens were not detected in burned *Spartina* marshes. Height of *Juncus* in burned plots was not significantly different from unburned plots by summer, corresponding to the recovery of abundances of sedge wren, whereas height of *Spartina* remained significantly shorter in burned than unburned plots for the duration of the study. In shrub/scrub wetlands in northern Minnesota, sedge wrens were more abundant on managed sites (managed sites were treated with combinations of shearing and burning) than unmanaged sites (Hanowski et al. 1999). Sites that had been sheared, but not burned were not significantly different than sites with a combination of burning and shearing within the previous 0-3 years. The time scale of this study was very coarse (i.e., categories of 3 years) so seasonal or yearly changes in wren abundance in these shrub/scrub wetlands could not be discerned, but provides a longer-term outlook on wren response to habitat changes.

Many icterids nest in tall, thick vegetation or trees, but forage in more open areas, accounting for the increase in abundance in burns immediately post-burn, and greater abundances in unburned areas during the breeding season. Boat-tailed grackles (*Quiscalus major*) in the Chenier Plains were observed in burned plots immediately post-burn, but not the following winter (Gabrey et al. 1999). Red-winged blackbirds (*Agelaius phoenicius*) were twice as abundant in burned as unburned plots immediately post-burn but were still present in burned areas the following winter. During the spring breeding and nesting season in these same study plots, icterids tended to be more numerous during the second spring after the burn than the first and third spring, but the differences were not significant (Gabrey et al. 2001). Vogl (1973) did not find any

difference in abundances of red-winged blackbirds after part of the shoreline of a pond was burned in the winter. Yellow-winged blackbirds (*Agelaius thilius*) in salt marshes in the Mar Chiquita Biosphere Reserve, Argentina were only detected in unburned *Spartina*, but did not differ in burn treatments in *Juncus* marshes (Isacch et al. 2004).

Secretive marsh birds typically require dense marsh vegetation for breeding and foraging. Flooding in river deltas is a natural disturbance that typically removes decadent vegetation and resets succession of vegetation. Changes in flood regimes of wetlands have negatively impacted many species adapted to these disturbances, including the US endangered Yuma clapper rail (*Rallus longirostris yumanensis*). Prescribed burns were conducted as a surrogate management tool for flooding during late winter or early spring in the Colorado River Delta over the course of six years and monitored for secretive marsh bird use (Conway et al. 2010). Detection probabilities were calculated to determine whether changes in vegetation structure affected detectability on control and burn plots and impacted interpretation of results. Yuma clapper and Virginia (*Rallus limnicola*) rails were more numerous in burned areas post-burn than pre-burn, an increase that only occurred in burned areas. As time since burn increased, the difference in abundance pre- and post-burn diminished. Virginia rails declined to pre-burn abundances faster than Yuma clapper rails. Other secretive marsh birds (California black rail (*Laterallus jamaicensis coturniculus*; listed as endangered in Mexico and threatened in California), sora (*Porzana carolina*), and least bittern (*Ixobrychus exilis*)) did not differ between burned and unburned areas. Conway et al. (2010) suggest that dense vegetation reduces foraging efficiency and prey availability. Also, rails are likely more susceptible to predation if they have to walk on top of matted

dead vegetation to reach foraging and nesting locations. Fire or flooding removes these thick mats of dead vegetation. Prior to this study, managers of the delta have not been allowed to burn habitat critical to and inhabited by an endangered species. Conway et al. (2010) demonstrated that prescribed fire in fact increases Yuma clapper and Virginia rail abundance without negatively impacting other secretive marsh birds.

Wilson's snipe (*Gallinago delicata*) typically avoid wetlands with dense, tall vegetation (Mueller 1999), suggesting that burns should be beneficial to snipe until vegetation regrows. Wilson's snipe were reported in burned areas by (Lynch 1941) though no direct comparison was made with unburned areas. Snipe were more numerous in burned than in unburned areas along the shore of a pond (Vogl 1973) and in isolated wetlands in the Rainwater Basin in Nebraska (Brennan et al. 2005). In Rainwater Basin wetlands, snipe were also observed in more burned wetlands post-burn than pre-burn (Brennan et al. 2005), corroborating evidence that snipe burned areas provide open areas for foraging.

A number of other species were observed during comparison of bird use of burned and unburned wetlands and can be grouped into categories of species that use open areas and species that prefer dense vegetation. Species that use open areas were more abundant in burned than unburned wetlands. Vogl (1973) reported higher abundances of common crow (*Corvus brachyrhynchos*), mourning dove (*Zenaida macroura*), northern cardinal (*Cardinalis cardinalis*) great blue heron (*Ardea herodias*), little blue heron (*Egretta cerulea*), snowy egret (*Egretta thula*), tricolored heron (*Egretta tricolor*), and other species on burned than unburned shorelines of a pond. Similarly, southern lapwings (*Vanellus chilensis*) used recently burned salt marshes in Mar

Chiquita Biosphere Reserve, Argentina, but were present only briefly in *Juncus* marshes and only until vegetation in *Spartina* marshes started sprouting (Isacch et al. 2004). Correndera pipits (*Anthus correndera*) were only detected in burned plots. Pipits were briefly observed in *Juncus* marshes during the first two months of surveys whereas in *Spartina* marshes they persisted for the duration of the study. Since burned *Spartina* did not regrow as quickly as *Juncus* (Isacch et al. 2004), species such as pipits which are typically found in grasslands may have benefited from the shorter vegetation, accounting for their persistence in burned *Spartina*. While it is likely that the reduction of vegetation provided additional areas in which these birds could forage, other aspects of the fire may have attracted these species to use burned wetlands.

Many other species typically found in wetlands with thick vegetation were not commonly observed in recently burned wetlands. Species typically associated with shrubs were more abundant on unmanaged than managed (i.e., shearing and burning) shrub/scrub wetlands whereas species that are associated with emergent vegetation wetlands were more abundant in managed wetlands (Hanowski et al. 1999). Common yellowthroat (*Geothlypis trichas*), which typically are described as skulking through marsh vegetation, were not seen in burns in the Chenier Plains along coastal southwestern Louisiana until the winter following early winter prescribed burns (Gabrey et al. 1999). The red-capped wren-spinetail (*Spartonoica maluroides*), a wetland-associated species, and freckle-breasted thornbirds (*Phacellodomus striaticollis*) appeared in *Juncus* marshes in Mar Chiquita Biosphere Reserve, Argentina three months post-burn (Isacch et al. 2004). Shortly thereafter, thornbirds were at similar abundances and by one year post-burn wren-spinetails was equally abundant in burned

and unburned *Juncus*. In *Spartina* marshes, wren-spinetails appeared four months post-burn, but remained at a lower abundance in burned than unburned *Spartina* for the year these plots were monitored. Crakes were only observed in unburned *Spartina* marshes in the year following spring burns. While dot-winged crake (*Porzana spiloptera*) were also observed in unburned *Juncus* marshes, speckled crake (*Coturnicops notata*) were never seen in *Juncus* marshes. Burns were only observed for one year so it is impossible to know whether crakes used recent burns sometime after the study finished. Had this study continued more than a year, differences in abundances of many species in *Spartina* plots might not have been seen. At the end of the study, *Juncus* marshes had recovered their vegetative structure, but *Spartina* marshes had not, likely resulting in differences of species presence and abundances noted between marsh types.

Patches of vegetation during and after a fire serve as refugia and potentially as a source for recolonization of the burned area. Nelson's sharp-tailed (in winter) and swamp sparrows (in summer) were only detected in burned plots that contained some unburned vegetation (Gabrey et al. 2001), suggesting that a complete burn that does not leave patches of vegetation may make the entire burned area unsuitable for these species. Similarly, dusky seaside sparrows (*A. mirabilis nigrescens*) were displaced for approximately six months after wildfires burned part of St. Johns NWR marsh in winter, but then defended territories within the burned area shortly thereafter (Baker 1974). Unburned patches appear to have provided cover for these species between the time when fires occurred and breeding. Black rails used unburned patches of vegetation within a prescribed burn conducted during the summer on the St. Johns National

Wildlife Refuge in Florida (Legare et al. 1998). A more complete winter prescribed burn (~90% of area burned) resulted in mortality of black rails that had taken refuge in wetter, vegetated portions of the marsh left by a previous burn (Legare et al. 1998).

Use of Burned Wetlands for Foraging

Opportunistic foraging during fire

Burning exposes prey resources for many species, making prey more vulnerable to predation than they are in dense vegetative cover. Blackbirds (Family Icteridae), swallows (Family Hirundinidae), gulls (Family Laridae), and raptors (Family Accipitridae) have been observed flying through smoke of a spring prescribed fire in coastal wetlands to catch prey such as insects and small mammals (Lynch 1941, Stevenson and Meitzen 1946, Tewes 1984). This is similar to observations during forest and grass fires where many avian species forage on prey fleeing the flames (Komarek 1969). This phenomenon likely occurs in most wetlands during fires and may serve as a beneficial resource pulse to species responding to the disturbance. To the best of my knowledge, the benefits of this behavior have not been quantified.

Foraging after fire

Burning of wetlands can enhance food resources for species, however, timing and availability of food resources is an important consideration. In coastal marshes in southeastern US wildlife refuges, Perkins (1968) and Givens (1962) found that fall to early winter burns resulted in succulent browse and heavy use of recently burned areas by geese. In the first study with a reported control of waterfowl response to burning, Gabrey et al. (1999) conducted five aerial surveys of burned and unburned plots for white geese (i.e., readily visible from the air) over 2 months beginning immediately after winter prescribed burns in the Chenier Plains. Ten flocks of white geese (lesser snow

and Ross's geese (*C. rossii*) were observed in burned sites (eight flocks) and in grit sites (2 flocks) adjacent to a burned area, ranging from 300 to 17,500 birds per flock, while no flocks were observed in unburned areas. Summer or early fall burns (in the Gulf Coast wintering grounds) often attract thousands of wintering snow geese that may forage on plant roots (Hoffpauir 1961). Gabrey et al. (1999) suggest that by removing above-ground vegetation through burning, plant roots were accessible to foraging geese. Consumption of roots will prevent plant regrowth if root stocks are reduced substantially (Hoffpauir 1961) and can shift species composition (Gauthier et al. 2004). Almost no studies of foraging benefits post-fire to birds other than waterfowl have been conducted. Marsh harriers (*Circus spilonotus*) did not hunt as much over burned sections of the Watarase Marsh, Japan during the first year post-burn as they did over unburned marsh area (Hirano et al. 2003). In the second year post-burn when reeds had regrown, harriers foraged equally over burned and unburned areas, indicating that their prey had returned.

Foraging during migration

Most research on the use of burned wetlands during migration has focused on waterfowl species. Many waterfowl species use recently burned areas in the season after the fire. Waterfowl used burned wetlands in the Sandhills of Nebraska during spring migration after prescribed burning in winter (Schlichtemeier 1967). Waterfowl use of the burn continued into summer and fall because of the open water and edge effect created by burning. In *Phragmites* stands in the Delta Marsh, a late summer prescribed burn substantially reduced stem density resulting in large congregations of waterfowl in the fall and heavy use by ducks for nesting for multiple years following the burn (Ward 1968). Brennan et al. (2005) explored the effect of spring prescribed burns near or up to

the edge of isolated wetlands in the Rainwater Basin in Nebraska. Pairs of burned and unburned wetlands were surveyed within seven days prior to and within seven days after the burn. Ducks and other waterfowl (excluding geese) were detected in burned and unburned wetlands pre- and post-burn, but did not appear to respond to burn treatments.

Timing of wetland fires appears less important for attracting migrating geese than other waterfowl due to differences in forage preferences. Prescribed burns in the Rainwater Basin were conducted after peak snow goose migration, yet geese were nearly twice as abundant in wetlands during post-burn than pre-burn surveys (Brennan et al. 2005). Migrating snow geese were observed in fewer burned wetlands post-burn than pre-burn, but were observed in an equal number of burned and unburned wetlands post-burn. Given that wetlands were surveyed within seven days post-burn, it is unlikely that geese were attracted by succulent new growth, but rather were foraging on readily accessible roots. Similar abundances of geese in burned and unburned wetlands post-burn suggest that while plant roots were a valuable “new” food resource, geese were not food limited in unburned wetlands. Alternatively, geese may have rested in burns because the burns are open, providing a clear line of sight to watch for predators. Wet meadows between the Tule and Little Tule rivers in northern California were burned in fall and surveyed for geese use the following spring (McWilliams et al. 2007). Geese made little use of the experimental blocks (2.3 ha) or the peninsula on which the experimental blocks were situated. When geese were present in the experimental blocks, Pacific greater white-fronted geese (*Anser albifrons frontalis*) foraged exclusively in the burned portions during evening feeding periods. The results of

Brennan et al. (2005) and McWilliams et al. (2007) indicate geese forage in burned areas due to reduction in vegetation, regardless of timing of the burn. Unburned vegetation likely impedes access to roots and tubers, a preferred food of many geese (Lynch et al. 1947). However, for other waterfowl species, timing of fire to produce beneficial changes in vegetation structure will impact wetland use by these species. During migration, many waterfowl forage on seeds and nutritious regrowth (e.g., van der Graaf et al. 2006) which needs time to grow and develop post-burn.

Use of Burned Wetlands for Nesting

Vegetative structure plays a big role in determining use of burned areas for nesting by many species. Male Louisiana seaside sparrows (*Ammodramus maritimus fisheri*) declined in abundance during the breeding season in the first year after a winter burn, but were more numerous in burned than unburned plots the second year (Gabrey and Afton 2000). Other sparrow species in this same habitat also used recently burned areas limitedly for nesting in the summer until the second year (Gabrey et al. 2001). Similarly, Cape Sable seaside sparrows (*A. m. mirabilis*) avoided burned areas after a fire burned nesting habitat in the Everglades in southern Florida (Taylor 1983, Curnutt et al. 1998, Walters et al. 2000, La Puma et al. 2007). Two years post-burn, Cape Sable seaside sparrows were detected in burned areas. Sparrows that were detected in the burned area during the first two years post-burn had territories on the edge of the burn and spent some time in the burn for “unknown reasons” (La Puma et al. 2007). It is likely that sparrows may have been exploiting food resources that were available in the burn and not in another sparrow’s territory in the unburned grass edge. Taylor (1983) observed Cape Sable seaside sparrows within one year of prescribed fire in unburned areas of the transect traversing the burn edge, suggesting that the fire caused the birds

to clump along this edge. Conversely, seaside sparrows in coastal Maryland had higher densities of territories and nests within one year after a winter prescribed burn than after longer durations since fire (Kern et al. 2012). Additionally, after more than five years without a burn, nest and territory density was 50% less than densities within the first year post-burn.

Once vegetative structure returned to pre-fire levels, sparrows nested in burned areas. In the Chenier Plains, dead vegetation coverage percentages were similar between burned and unburned plots by the second year and Louisiana seaside sparrows were using recently burned habitat (Gabrey and Afton 2000). In the second year, average nesting activity indicators (i.e., an index of sparrow productivity including adults with nesting materials or food, copulation, nests, flightless juveniles) per plot were higher in burned than unburned plots, suggesting that the renewal of vegetation benefited this species once vegetation structure recovered. By the third year in the Everglades, re-growth provided appropriate vegetation structure in the burned area and Cape Sable seaside sparrows were found in densities similar to adjacent unburned areas, formed territories, and nested in the burned area (La Puma et al. 2007). For most species with large populations, a disturbance event impacting 1-2 breeding seasons in a small area is not considered much of a concern. However, for the endangered Cape Sable seaside sparrows, fire occurring frequently or over a large area is viewed as a threat to the longevity of this species. Knowledge of sparrow movements as a fire burns Cape Sable seaside sparrow breeding habitat would resolve the question of whether fire creates a displacement or mortality event for this species.

Timing of burns can be detrimental to nesting species if nests are destroyed or fledglings are unable to flee from the fire. Burning too late in the spring can harm nesting ducks (Cartwright 1942). A spring wildfire in the Delta Marsh in Manitoba caused nest failure and mortality of hens and ducklings (Ward 1968). Thus, Ward (1968) suggested burning in summer just after completion of nesting. Summer burns may damage nests of late nesting mottled ducks (*Anas fulvigula*; Hoffpauir 1961), but can be very beneficial if conducted late enough. Ward (1968) conducted a late summer prescribed burn to open *Phragmites* stands in the Delta Marsh. In multiple subsequent years, ducks heavily used the area for nesting. Winter burns occurring five months prior to the nesting season do not appear to result in higher depredation rates (Gabrey et al. 2002).

Consumption by fire of nesting substrate may impact nesting locations of many species. Fires occurring prior to the nesting season remove readily available nesting substrate for wading birds (Family Ciconiiformes; Giles and Marshall 1954, Bray 1984). At the Bear River Migratory Bird Refuge in Utah, Bray (1984) compared densities of vegetation during the summer 4 and 16 months post-burn to a wading bird colony under the same water control management scheme. Fire eliminated all dead stems of *Scirpus acutus* for at least the first four months. Great blue herons, snowy egrets, and black-crowned night-herons (*Nycticorax nycticorax*) nested only in stands of *Scirpus acutus* with a combination of dead and live stems. While live stem density 4 and 16 months post-burn was similar to stem density in colonies, dead stem density 16 months post-burn was still less than in colonial nesting areas. The authors suggest that nesting material and nest site availability might be limited. Wading birds did not nest at the

burned site (pre- or post-burn) so conclusions regarding live vs. dead stem density cannot be drawn. American coot (*Fulica americana*) nest success was reduced post-burn because fire burned vegetation used for nest material and water levels rose (Austin and Buhl 2011). Nest success declined post-burn in the year following the burn, approaching a similar rate of nest success that resulted from grazing. While nest success in the burn treatment was already declining pre-burn, fire did not benefit the coots in any way.

Nest site selection can impact the likelihood of nests being damaged or eliminated by fire. Red-crowned cranes (*Grus japonensis*) show a preference for nesting in areas with tall reeds (Wu and Zou 2011). While cranes nested in more diverse habitats after a wildfire, they typically avoided burned areas because of the change in vegetation, with many birds nesting more than 1.5 km from burned areas (Zou et al. 2003). Cranes occasionally nested in burns, but Wu and Zou (2011) suggest cranes also avoid burned areas because these white birds are more visible in a blackened habitat. No mention was made of how soon cranes return to these burned areas. Rather than nesting in *Scirpus* stands, wading birds in the Everglades nest in colonies in tree islands covered with woody vegetation composed primarily of willow (*Salix caroliniana*), buttonbush (*Cephalanthus occidentalis*), and/or cypress (*Taxodium* spp.). Two separate wildfire events burned around a large wading bird colony during breeding season, corresponding with dry down near the end of the dry season (Epanchin et al. 2002). Both fires burned the sawgrass (*Cladium jamaicense*) and cattail (*Typha* spp.) surrounding the colony, but did not burn the buttonbush and willows on the island. The shallow water present within the colony likely protected it from burning. Epanchin et al.

(2002) reported no abandonment of nests or loss of chicks after either of the wildfires that burned around the colony.

Fire occurring in nesting areas may be detrimental to nest success for species requiring vegetation structure to conceal their nests from predators and reduce exposure of the eggs to the environment. In coastal Louisiana marshes, Gabrey et al. (2002) studied depredation rates on artificial seaside sparrow nests containing *Coturnix* quail eggs and artificial mottled duck nests in burned and unburned plots five months after winter prescribed burns. Depredation rates of artificial sparrow nests were high, but not significantly different between burned and unburned plots and not different pre- vs. post-burn (Gabrey et al. 2002). Depredation rates of duck nests did not differ between burn treatments. Vegetation structure did not differ between burn treatments five months post-burn, indicating that if burns are conducted so vegetation has time to recover sufficiently, nesting waterfowl likely will not be negatively impacted by predators taking advantage of recent burns. Almario et al. (2009) compared depredation rates of artificial and natural seaside sparrow nests in burned and unburned areas in tidal salt marshes in Blackwater National Wildlife Refuge, MD after winter prescribed burns of annually burned areas. In the first year, depredation rates were higher for natural and artificial nests in the incubation stage in burned than unburned areas, and artificial nests were depredated more than natural nests. Depredation rates of artificial nests in burned areas were similar between studies (Gabrey et al. 2002, Almario et al. 2009). In the following year, more precipitation resulted in greater biological productivity, more standing dead vegetative cover, and a difference in nest placement (Almario et al. 2009). These differences are likely why depredation rates did not differ between burn

treatments the second year. Kern et al. (2012) reported that nest survival was highest in years with high *Spartina* cover. However, fledging density was similar across all years post-burn, indicating that more predation may have impacted recently burned areas that otherwise had higher densities of territories, nests, and eggs. Vergeichik and Kozulin (2006) speculate that removal of dead vegetation and fresh green vegetation which normally camouflages nests of the aquatic warbler (*Acrocephalus paludicola*) resulted in increased egg mortality due to predators, especially the abundant shrews in these Polesseye lowland mires, Belarus.

Besides vegetation structure, food resources and water quality conditions after a burn can influence use of wetlands for breeding purposes. Haszard and Clark (2007) conducted surveys and sampled peatland bogs and fens to determine how a wildfire influenced white-winged scoter (*Melanitta fusca*) breeding and brood success. Three years post-fire, Haszard and Clark (2007) aerially surveyed for scoter pairs and broods in peatland bogs and fens embedded in burned and unburned upland areas in and adjacent to the Mackenzie River Delta, Northwest Territories, Canada. About 2 weeks after brood surveys, Haszard and Clark (2007) collected water samples from a subset of the surveyed wetlands for analysis for nutrient and dissolved oxygen concentration and water color and measured conductivity and amphipod abundance in each sampled wetland. While scoter pair density was correlated with higher amphipod abundance, no correlation of scoter pair density or brood occurrence with water chemistry or burn status of the upland was reported. Amphipod abundance was also not related to burned or unburned forest surrounding the wetland. Phosphorus limitation in this area may account for the lack of a response three years post-fire. Available nutrients likely were

utilized immediately post-fire and thus were distributed and unavailable three years later to increase productivity.

Herpetofauna

Herpetofauna are impacted by fires occurring in terrestrial and wetland ecosystems (Russell et al. 1999, Pilliod et al. 2003). While many studies have illustrated the effect of fire in upland habitats, studies of fire effects on amphibians in wetlands are sparse and on reptiles are essentially non-existent. Herpetofauna use wetlands for breeding, development, and refuge. I found 2 reptile and 11 amphibian studies that describe fire effects on herps, including 3 articles that are responses to the initial article. Most studies of fire effects on amphibians go beyond presence and abundance post-fire to examine habitat selection by these species.

Indirect Effects of Prescribed Burning

Plow lines have been built around wetlands embedded in pine flatwoods to avoid peat fires and negatively impacting the wetland (Russell et al. 1999, Bishop and Haas 2005). When water levels drop, plow lines that were previously submerged within the wetland can become a trap for developing larvae. Bishop and Haas (2005) found >500 desiccated tadpoles in a previously submerged plow line ringing a wetland. Additionally, these plow lines may provide a false signal for terrestrially ovipositing flatwoods salamanders seeking a depression close to the wetland (Russell et al. 1999).

Presence and Abundance

Herpetofauna use wetlands for foraging, cover, and hibernation, but there is almost no information on effects of fire on species using wetlands. Babbitt and Babbitt (1951) found nearly three dozen injured or dead Florida box turtles (*Terrapene carolina bauri*) and 10 eastern diamondback rattlesnakes (*Crotalus adamanteus*) in Dade

County, Florida on a limestone ridge in an area with peat and thick understory vegetation that had burned. It is unclear from the note if the burn occurred in or adjacent to a wetland, but given the proximity of the Everglades, it is likely that this area was at least a short hydroperiod wetland. In response to low intensity prescribed burns in bottomland hardwood forests in Georgia, reptile species richness did not differ between burned and unburned stands (Moseley et al. 2003). However, reptile abundance and diversity was greater in burned than unburned areas, likely because reptiles had more thermoregulatory options as a result of decreased ground cover. It is apparent that more research of reptile response to fires in wetlands is needed.

Amphibian richness, abundance, or diversity within the first year post-burn typically does not increase positively. Moseley et al. (2003) sampled the amphibian community in bottomland hardwood stands in Georgia 6-10 months after low-intensity winter prescribed burns. Amphibian richness, abundance, and diversity did not differ between burned and unburned treatments, likely because volumes of coarse woody debris providing cover remained post-fire. Occupancy of isolated wetlands in Montana by long-toed salamanders (*Ambystoma macrodactylum*) and Columbia spotted frogs (*Rana luteiventris*) did not change after summer wildfires burned their wetlands (Hossack and Corn 2007). Salamanders may have increased occupancy of burned wetlands post-burn, but support was weak for these models. Boreal toads (*Bufo boreas*) colonized wetlands post-burn, but were not breeding in these wetlands before the fire. Conversely, Schurbon and Fauth (2003) indicate that fire has immediate and short-term negative impacts on amphibian abundance and diversity in ponds embedded in southeastern pine flatwoods in Francis Marion National Forest, South Carolina. Many species of

amphibians were not detected the first year after a fire, however, the interpretation of these results is limited given that this study was conducted for only one season post-burn. Using historic fire data, Schurbon and Fauth (2003, 2004) showed that richness increased with time since the wetland had burned, resulting in the authors recommending that fire frequency should be decreased and burn season switched from winter to summer. This interpretation has been questioned on the grounds of short study period, fire history of the study sites, and hydroperiod lengths (Means et al. 2004, Robertson and Ostertag 2004).

Breeding

Amphibian species have a variety of requirements when selecting breeding sites that impact whether burning wetlands may be beneficial or not. Boreal toads did not breed in isolated, montane wetlands before they were burned, but used burned wetlands for breeding the year after the burn (Hossack and Corn 2007). After the first year post-burn, boreal toad abundance declined in these wetlands over the next two years to zero. No boreal toad larvae were found in unburned wetlands, suggesting that boreal toads benefit from fire burning wetlands. In a follow up study, Hossack and Corn (2008) investigated how water temperature post-burn influenced breeding site selection by boreal toads in years two and three after a wildfire in Glacier National Park. However, unburned wetlands (which were unoccupied by toads due to selection of sampling sites) were warmer than burned wetlands despite open canopy over all sites. Toads did not appear to select against warmer wetlands. Hossack and Corn (2008) note that they have never found boreal toads breeding in well-shaded wetlands, suggesting that sunlight or an open canopy is more important for this species than temperature. Boreal toads appear to prefer open canopy as long as they also have ground cover to

escape predators and maintain water balance (Guscio et al. 2008). Like boreal toads, Florida bog frogs (*Lithobates okaloosae*) require periodic fires in their breeding wetlands to maintain vegetation conditions conducive to calling (Gorman and Haas 2011). Calling sites for this species had more submergent vegetation and lower water depths than what the sympatric bronze frog (*L. clamitans clamitans*) selected, and may be a result of occasional fire in the wetland (Enge 2005, Gorman and Haas 2011). Interestingly, the bronze frog selects for sites with appropriate water depth and flow conducive to oviposition and egg development, quite different from the habitat selected by Florida bog frogs.

Periodic fire may be important for maintaining habitat necessary for larval development of amphibians. Periodic fires burn bogs embedded in longleaf pine forests in the southeastern US, removing woody vegetation and supposedly maintaining hydroperiod length by reducing evapotranspirative losses (Means and Moler 1979). These fires reset succession of shrub bogs to herbaceous bogs, thereby benefiting larval Pine Barrens treefrogs (*Hyla andersonii*) typically found in herbaceous bogs. While adult treefrogs use bogs with woody vegetation, the additional woody vegetation is not good larval habitat. Similarly, larval flatwoods salamanders (*Ambystoma cingulatum*) may benefit from fire in wetlands by reducing woody vegetation in the canopy (Russell et al. 1999, Pilliod et al. 2003, Bishop and Haas 2005). Bishop and Haas (2005) provide indirect evidence that burning wetlands during the summer to open the canopy may be beneficial to developing larval flatwoods salamanders, potentially due to some combination of warmer water, a change in predation risk, more food, and

higher dissolved oxygen concentrations under open canopies. However, there is still no direct evidence that flatwoods salamanders benefit from fire burning their wetlands.

Lessons Learned

Fire is an important process in wetlands that resets habitat conditions for wildlife either via elimination of forbs and woody vegetation (short-term changes) or by burning peat and creating deep, open water habitats (long-term changes). Direct mortality events in wetlands appear to be rare, just like in upland habitats (Whelan 1995). Indirect effects of fire relate to removal of vegetation, change in food resources, and habitat changes that affect breeding. Specifically, fire initially reduces abundances of species that prefer dense vegetation for cover and nesting. Conversely, fire increases abundances of species that utilize open habitats for breeding and foraging. However, while we can predict responses of many species according to their life histories and specific requirements for cover, food, and habitat for breeding and development, management is best conducted using data rather than inferences.

Appropriate vegetative structure is important for habitat occupancy by wildlife (e.g., Gabrey et al. 2001, Gabrey and Afton 2004) and impacts nest depredation rates (Gabrey et al. 2002, Almario et al. 2009). Vegetative cover serves multiple purposes including nesting materials, supports, and cover, protection from predators and the elements, and food resources (i.e., seeds, fresh growth, and habitat for insects and small mammals). Fire temporarily alters these conditions until vegetative cover regrows. Species such as seaside sparrows and wrens that typically are found in habitats with dense vegetative structure are not found in a recently burned area until vegetative structure returns to pre-burn level. Evidence of preference for vegetative cover was seen in seaside sparrow use of burn edges and of patches of vegetation within burn

units (Taylor 1983, Gabrey et al. 1999, La Puma et al. 2007) and black rail use of unburned patches of marsh (Legare et al. 1998). Conversely, species that prefer open areas with limited vegetative structure for at least part of their daily activities such as waterfowl and boreal toads used burned areas extensively until vegetative structure becomes too dense. However, even for many species that prefer dense vegetation, vegetation can become too dense and impede movements. For example, Conway et al. (2010) noted that rails walk on top of thick mats of dead vegetation where they are more exposed to predators than walking through recently disturbed habitat.

Food resources such as fresh regrowth, mast, or arthropods may explain use or disuse immediately post-burn, yet the response of wildlife to burns in wetlands to changes in food resources has not been well studied. While it is apparent from these studies that geese and birds of prey such as harriers respond to fire due to food resources, it is likely that many other species (e.g., icterids, sparrows) use burns for food resources. Combustion of grass and forbs immediately exposes roots to foraging by many herbivorous species such as geese and continues as fresh shoots emerge, attracting many other herbivores such as muskrats and deer. Fresh forage is often more digestible and of higher nutritional quality (Smith et al. 1984), providing a valuable source of nutrition for many species. Mast production may take much longer to produce (Lyon et al. 2000) although seeds that have already dispersed may be immediately available once the overstory is burned. Invertebrate response to fire varies in magnitude and in timing (e.g., de Szalay and Resh 1997, Benson et al. 2007, Hochkirch and Adorf 2007, Munro et al. 2009), but increased abundance of many invertebrate species benefits many avian species foraging for invertebrates. Henslow's sparrows wintering in

bogs responded strongly to frequency of grass seed stalks and forb density as predictors of bog occupancy (Tucker and Robinson 2003). The winter diet of this species is not well known so seeds or arthropod density (using forb density as an indicator of arthropod density) may be driving bog occupancy. Specific studies should be undertaken to describe wildlife response to changing food resources depending on season of burn, wetland conditions, and frequency and severity of fires.

When fire in wetlands removes vegetation, breeding efforts of amphibians typically benefit while birds may or may not benefit. Fire reduced canopy cover over many wetlands, benefiting larvae of many amphibian species. Canopy cover impacts temperature which is important to developing larvae (Niehaus et al. 2006), typically increasing the rate of metamorphosis until temperatures stress larvae. For birds, environmental effects do not appear to impact nests like they do for amphibians, However, depredation of nests post-burn may result. Recent burns do not appear to impact predation rates of bird nests (Almario et al. 2009), but differences in predators may affect nest success (Vergeichik and Kozulin 2006, Kern et al. 2012). Vergeichik & Kozulin (2006) note that shrews forage by smell, sound, and touch, making them more efficient at finding nestlings rather than eggs. Similar predators may have reduced fledgling densities to be equal between burned and unburned plots despite higher egg densities in burned areas in their study (Kern et al. 2012). To my knowledge there are no studies describing the effects of fire on nest predators such as small mammals or mesopredators.

In upland habitats, patches and mosaics are increasingly recognized as important aspects to include in management of ecosystems. Many wetland-dependent species

benefit from burns that leave unburned patches of habitat as refugia (e.g., Legare et al. 1998, Gabrey et al. 1999, 2001). Patchy burns can provide these refugia while also controlling vegetation density and cover. Waterfowl need a combination of shallow and deep open water areas for feeding, rearing broods, and avoiding predators, but also seek dense vegetation during nesting as a means of avoiding predators. Ward (1968) recommended burning sections of the marsh in order to leave sufficient nesting habitat available for ducks. Diving ducks primarily use open water areas in marshes while geese, using wetlands during migration or for winter, seek food resources such as succulent new regrowth. For species that prefer recently burned areas, patchy burns meet these habitat requirements and include cover for avoiding predators, particularly if woody debris for herps is left after a fire. At the same time, patchy burns also meet the needs of other species when unburned patches are left standing. By creating refugia, fewer birds are displaced by the burn. There has been no work in wetlands to quantify the size, number, or distribution of refugia post-burn to benefit species. Purposely creating refuges within a burn will likely require extensive effort by managers. To overcome this, research is needed to determine burn conditions conducive to naturally creating refuges via the burn or extensive effort during fire operations.

The effects of wildfires and prescribed burns are often different due to season, severity, and other conditions. Most of the studies I reviewed were conducted after prescribed burns outside of the natural fire season. Thus, our understanding of fire effects on wildlife is relevant to our current management scheme, but does not reflect historical ecosystem effects. Historical fire effects likely provided crucial habitat for species, whether through canopy removal benefiting larval amphibians (Bishop and

Haas 2005) or open water habitat for waterfowl (Ward 1968). Peat fires, which sometimes occur with wildfires, can significantly change a wetland and may be important in managing certain species (Ward 1968, Norton and De Lange 2003). However, peat burns are avoided during prescribed burns because they are impossible to control. Managing wetlands to allow natural peat burns to occur is necessary to maintain many wetland communities (Reardon et al. 2007). Pre-burn data are typically unavailable for wildfires and control sites may not be comparable to burned sites despite being adjacent to the burned area, making interpretation of fire effects challenging. However, more studies on wildfires are needed to address questions of effects on wildlife post-burn.

Season of burn was frequently discussed in the early fire literature when burns were commonly conducted to benefit waterfowl. Effects of fire due to frequency, severity, and time since burn are equally important. A recent review of fire-dependent upland avian species in longleaf pine forests highlighted the differences in responses to fire as a result of season of burn (Cox and Widener 2008). Historically, prescribed burns in wetlands were conducted sometime from early fall to early spring to avoid biological (e.g., burning nests) and environmental (e.g., burning peat) impacts. However, most natural fires occur during late spring and summer when lightning is most prevalent (e.g., Gunderson and Snyder 1994, Slocum et al. 2007). At this time of year, wetlands often contain much water, reducing the potential for peat burns. If prescribed burns are conducted in mid-spring or summer, nesting, breeding, and requirements of eggs or juveniles inhabiting the wetland must be considered in order to avoid eliminating a sensitive cohort while achieving the goal of benefiting target species. Continuance of

prescribed burning in other seasons also must consider species movements and resource and habitat needs. Bishop and Haas (2005) suggested that winter prescribed fires in upland areas around wetlands may negatively impact the migration of flatwoods salamanders to wetlands at this time of year for initiation of breeding.

Most studies I reviewed were conducted within 2 years post-burn although a few exceptions carried studies 4-6 years (Taylor 1983, La Puma et al. 2007, Conway et al. 2010). While vegetation in some wetlands recovers rapidly (e.g., 1-2 years; Loveless 1959, Gabrey et al. 1999), long term studies are necessary to determine the trends species show in relation to vegetation recovery (e.g., Gabrey et al. 2001, La Puma et al. 2007, Conway et al. 2010). The fire return interval is typically longer than complete vegetation recovery. By monitoring species from pre-burn through vegetation recovery post-burn until at least the next burn, fire frequency can be adjusted if the current fire regime negatively impacts species. Studies presenting 1 year of data are informative, however they may result in misleading conclusions and recommendations and should qualify results as preliminary until more research over a longer time period is conducted.

In order to understand the effects of fire on wetland-dependent wildlife, studies need to include controls whether side-by-side comparisons (i.e., burn vs. control) or temporal (i.e., pre- vs. post-burn) comparisons. Early studies advocating use of fire in marshes for the enhancement of waterfowl foraging and nesting areas were typically incomplete in their description of burn methods, description of environmental and confounding variables, quantification of response, and management techniques. However, some, like Ward (1968), made an effort to provide their methods and means of comparison by describing their ignition conditions and process so others could

replicate the burn prescription. Yet, pre-burn data and replication were not included in the report of the study results. Before-after-control-impact (BACI) designs are well-suited to studies of fire effects because they incorporate spatial and temporal comparisons (Underwood 1994). Conway et al. (2010) used this type of design to determine trends of rail abundances in plots prior to and after conducting prescribed fires. Furthermore, the importance of designing studies that incorporate knowledge of fire history and regime, life history requirements, and appropriately quantified response to fire by species (Means et al. 2004, Robertson and Ostertag 2004, Schurbon and Fauth 2004) cannot be overemphasized, as this is critical when providing recommendations to managers. While long-term studies such as the study by Conway et al. (2010) may be difficult to conduct when time and money are limited, an understanding of bird response as vegetative cover and insect populations recover post-fire is necessary to appropriately implement fire as a management tool in wetlands. Many of the studies of Cape Sable seaside sparrows were terminated shortly after sparrows in burned and unburned areas became similar in abundance. Whether the trend in abundance continued to increase or peaked was not determined, but is important for implementing or adjusting a prescribed fire regime, particularly if target species are a species of concern.

Basic presence and abundance information is important to initially focus research on important questions, but more extensive, complex studies are needed. Most studies I reviewed report solely on presence/absence, abundance, and duration of use of species post-burn. Reptiles and mammals were essentially unrepresented in the wetland fire effects literature. Only a handful of studies looked at amphibian or avian breeding or

nest site selection, larval development, or depredation rates of nests. A series of experiments by Gabrey and coauthors (Gabrey et al. 1999, Gabrey and Afton 2000, 2001, Gabrey et al. 2001, Gabrey et al. 2002, Gabrey and Afton 2004) on Louisiana seaside sparrow response to winter prescribed fires in the Chenier Plains provide a great illustration of the type of studies needed to understand effects of fire on species. With the exception of Gabrey's work and studies on boreal toads (Hossack and Corn 2007, Guscio et al. 2008, Hossack and Corn 2008, Hossack et al. 2009), few follow-up studies of species responses to fire in wetlands have been conducted once presence and abundance data were collected. Saab and Powell (2005) called for a move towards increasing our understanding of fire effects on reproductive success, nest survival, and changes in population. I echo this call for fire effects research on all wetland-dependent wildlife. While we now know that certain groups of species are attracted to or avoid burns in wetlands one to two years post-burn, we still cannot confidently point to the causal mechanism for many of these species, whether mortality, vegetative cover requirements, food resources, or other factors.

A number of overarching questions exist regarding fire effects on wetland-dependent wildlife. I highlight some of them here.

How do mammals respond to fire in wetlands? A number of small mammal species inhabit wetlands, but fire effects on most of these species have not been studied. Given changes in vegetation density and structure, I would expect many of these species to respond similarly to wrens and sparrows and avoid recently burned areas until vegetation recovers. However, some species (e.g., Florida salt marsh vole (*Microtus pennsylvanicus dukecampbelli*)) are adapted to daily disturbances (i.e., tides) and may

have a different strategy. Other mammals should benefit from fresh vegetative growth with higher nutrient content. I found almost no studies of non-domesticated herbivorous mammals in wetlands. This could be a factor of the type of wetlands, primarily salt marsh, that research of fire effects on wildlife has been conducted in. An understanding of the mammal community is important for the sake of managing for mammals, to understand the impact of mammal populations on bird nest predation rates, and as a food source for species.

How do reptiles respond to fire in wetlands? Reptiles use wetlands for a variety of purposes, like other species. However, I only found one study specifically investigating fire effects on reptiles in wetlands, which indicated snakes may benefit due to increased thermoregulatory opportunities. Additionally, turtle mortality near a wetland was reported (Babbitt and Babbitt 1951), indicative that some species may be negatively impacted by fire if refugia are not available. Deep peat burns may be important for turtles to maintain deep open water areas, however use of fires to maintain conditions in wetlands appropriate for use by turtles has not been studied.

How does fire control of food resources affect species response to fire? While much of the emphasis throughout this review was placed on vegetative density and structure, it is not entirely clear which environmental factors dictate species response to fire. Vegetative cover provides protection from predators, serves as breeding habitat, and is a source of food resources for many species, whether directly or indirectly. Fire temporarily alters these conditions promoting regrowth and a change in habitat structure and composition. Invertebrate response to changes in vegetation, microclimate, and debris, impacts their availability to species preying on them. An understanding of these

mechanisms will help inform management decisions regarding burn season, frequency, and severity.

How do peat fires impact wildlife use of wetlands post-burn? Peat fires typically occur during drought conditions in the natural fire season, but are actively avoided by limiting implementation of prescribed burns to times when water levels protect peat. However, peat burns maintain wetland communities by resetting succession and creating open water habitats favorable to some species. Suppression of peat burns may negatively impact wetlands and the species utilizing them. Additionally, peat fires are important in maintaining wetland characteristics and vegetative communities (i.e., Atlantic white cedar) and suppression of peat fires alters these wetlands and affects the wildlife that use these fire-maintained habitats.

How do fires impact individual movements and long-term wildlife population trends? Individual animal movements and population trends related to fire in wetlands remains unknown. Much discussion regarding mortality vs. dispersal of species due to fire and the impacts on the population has occupied reviews of species such as the Cable Sable seaside sparrow. Yet, to my knowledge no telemetry of individuals has been conducted to confirm or refute direct negative fire impacts that would also negatively impact a small population. Similar studies should be done on other species to better understand how species respond to fire. Studies of responses to fire by many species need to be conducted so we understand how prescribed burns and wildfires impact target and non-target species.

Table 2-1. Selected references of fire effects on wetland-dependent avian species.

Species	Wetland Type	Length of Study	Fire Type	Season of Fire	Use of Wetland	Response to Burns	Comments	
<u>Sparrows</u>								
Cape Sable seaside sparrow (<i>Ammodramus maritimus mirabilis</i>)	Everglades; sawgrass (<i>Cladium jamaicense</i>)	4 yrs post-fire	W	late dry season (May)	breeding	primarily avoided for first 2 yrs; 3 yrs post-fire densities & territories similar to unburned; nesting start 3 yrs post-fire	appropriate veg structure returned 3 yrs post-burn; suggested need for refugia & more time between burns (i.e., 10+ yr)	a
Cape Sable seaside sparrow	Everglades; <i>Muhlenbergia</i> & sawgrass (<i>Cladium jamaicense</i>)	4 yrs post-fire	W	winter Rx & June lightning fire	breeding	deeper soil: return in 2 nd yr & maybe peak in yr 4; shallow soil: returning in yr 4		b
Dusky Seaside Sparrow	St. Johns NWR, FL; salt marsh	~1 yr	W	winter	breeding	returned to burned area 6 mo. post-burn to set up & defend territories	3 birds banded in unburned habitat 900 m from banding location	c
Louisiana seaside sparrow	Chenier Plains, LA; brackish & salt marsh	3 breeding seasons	Exp	winter (mid-Jan.)	breeding	1 st yr: male abundance increased in season; 2 nd yr: more males in burn; nesting lower in burn in 1 st yr, but 2 nd yr higher in burn	dead veg cover recovered in 2nd yr - likely why nesting so much better second yr	d

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire Type	Season of Fire	Use of Wetland	Response to Burns	Comments	
seaside sparrow	Chenier Plains, LA; brackish & salt marsh	2 winters	Exp	winter (Dec., early Jan.)	cover	not found in burns until 2 nd yr	e	
seaside sparrow	Chenier Plains, LA; brackish & salt marsh	3 breeding, 1 pre & 2 post	Exp	Winter (Dec., early Jan.)	nesting	abundance dropped in burned plots & then increased 2 nd yr post burn	positively correlated with dead veg & <i>S. patens</i>	f
seaside sparrow	Chenier Plains, LA; brackish & salt marsh	2 breeding, 1 pre & 1 post-burn	Exp	winter (mid-Jan)	nesting	(artificial nests) high depredation, but no diff between yrs or trmts	veg cover 5 mo. post-burn similar to pre-burn so likely reason for no difference	g
seaside sparrow	Blackwater NWR, MD; tidal marsh	2 breeding seasons	Rx	winter	nesting	nest depredation high during incubation, total depredation did not differ between trmts, next yr showed no differences	artificial nests were depredated at much higher rate in burn than unburned	h

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire * Type	Season of Fire	Use of Wetland	Response to Burns	Comments
seaside sparrow	Blackwater NWR, MD; tidal marsh	5+ yrs	Rx	winter	nesting	<1 yr post-burn, highest territory and nest density; 50% lower nest and territory density 5+ yr than <1 yr post-burn; egg density higher <1 yr than 3-4 yr post-burn; no fledging density difference	percent <i>Spartina</i> cover and year explained nest success; predation may have caused depression of fledging density in recent burns
Nelson's sharp-tailed sparrow	Chenier Plains, LA; brackish & salt marsh	2 winters	Exp	winter (Dec., early Jan.)	cover	found in patches of unburned veg in one burn station	
sparrows	Chenier Plains, LA; brackish & salt marsh	3 breeding seasons	Exp	winter (Dec., early Jan.)	foraging nesting	2 nd yr post-burn 2x more than 1 st yr, but no diff with 3 rd yr	
swamp sparrow	Chenier Plains, LA; brackish & salt marsh	2 winters	Exp	winter (Dec., early Jan.)	cover	found only in stations with bunch of unburned veg	
Henslow's sparrow	AL & FL; Gulf Coast pitcher plant bogs	2 winters	NA	growing, dormant	wintering	higher abundance 1 st yr post-fire; densities post-growing season higher thru more yrs	

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire Type	Season of Fire	Use of Wetland	Response to Burns	Comments
sparrows (transients)	Tall Timbers Research Station – Gannet Pond	4 mos.	Exp	winter		song & swamp sparrow had more in unburned shoreline	j
grassland yellow-finch	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	only in unburned <i>Spartina</i> ; 1 mo. Post- <i>Juncus</i> burn	k
great pampa-finch	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	only in burned <i>Spartina</i> ; 2 mo. Post- <i>Juncus</i> burn	k
<u>Wrens</u>							
marsh wren	Chenier Plains, LA; brackish & salt marsh	2 winters	Exp	winter (Dec., early Jan.)	cover	found more in unburned immediately post-fire although this increased in 2 nd yr	other birds detected on <5% of surveys
sedge wren (<i>Cistothorus platensis</i>)	Chenier Plains, LA; brackish & salt marsh	2 winters	Exp	winter (Dec., early Jan.)	cover	not found in burns until 2 nd yr, but still primarily in unburned	e
sedge wren	Northeast MN; scrub/shrub	1 yr, but 0-3+ yr fires	Rx	NA	breeding	highest abundance on burned sites	time scale very coarse in this study
grass wren (<i>Cistothorus platensis</i>)	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	only in unburned <i>Spartina</i> ; 4 mo. Post- <i>Juncus</i> burn, 6 mo. Similar abundance	k

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire Type	Season of Fire	Use of Wetland	Response to Burns	Comments
wrens	Chenier Plains, LA; brackish & salt marsh	3 breeding seasons	Exp	winter (Dec., early Jan.)	NA	no diff	i
<u>Wetland Associated spp.</u>							
common yellowthroat	Chenier Plains, LA; brackish & salt marsh	2 winters	Exp	winter (Dec., early Jan.)	cover	not found in burns until 2 nd yr	unburned patches provide cover for small birds e
red-capped wren-spinetail	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	appeared 4 mo. Post-burn, but lower abundance than unburned <i>Spartina</i> ; 3 mo. Post- <i>Juncus</i> burned; similar abundance btwn habitats 1 yr post- burn	<i>Juncus</i> recovered structure within 1 yr, but not <i>Spartina</i> k
emergent wetland spp.	Northeast MN; scrub/shrub	1 yr, but 0-3+yr fires	Rx	NA	breeding	more abundant on managed sites, includes sheared sites	i
shrub/forest spp.	Northeast MN; scrub/shrub	1 yr, but 0-3+yr fires	Rx	NA	breeding	more abundant on unmanaged sites	i

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire Type *	Season of Fire	Use of Wetland	Response to Burns	Comments
southern lapwing	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	in burn only until <i>Spartina</i> sprouted; first in <i>Juncus</i> , but brief	k
songbirds, but some others	Lake Victoria, Uganda; papyrus swamps	1 yr	NA	NA	foraging other	generalist spp. use burns more, but papyrus-reliant spp. not present	z
aquatic warbler (<i>Acrocephalus paludicola</i>)	Belarussian Polesye; fen marshland	1 yr obs.	NA	spring	nesting	suggest that lack of dead veg and green grass that egg mortality increased due to predation	af
red-crowned crane (<i>Grus japonensis</i>)	Zhalong Nature Reserve, China; reed swamp	NA	W	fall, spring	nesting foraging	avoid blackened burn, were farther from burned area with dense reeds nearby for concealment	aa
red-crowned crane	Zhalong Nature Reserve, China; reed swamp	NA	H	fall, spring	nesting	prefer tall reeds, may nest in burned areas	ad
“transients”, songbirds, dove	Tall Timbers Research Station - Gannet Pond	4 mos.	Exp	winter		all had more on burned shoreline	j

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire * Type	Season of Fire	Use of Wetland	Response to Burns	Comments	
"residents", crow, cardinal	Tall Timbers Research Station - Gannet Pond	4 mos.	Exp	winter		all had more on burned shoreline	j	
correndera pipit	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	in burn only, first in <i>Juncus</i> & then persisted	k	
Hudsons canastero	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	seen first months post-burn & then absent	k	
freckle- breasted thornbird	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	appear 3 mo. post- <i>Juncus</i> burn; similar abun btwn habitats 1 yr post- burn	k	
gulls, swallows	Chenier Plains, LA; salt marsh	obs.	Exp	Fall	foraging	catching insects in smoke of fire	m	
marsh harrier	Watarse Marsh, Japan; reed marsh	2 winters	W	winter	wintering breeding	flew less over burned area 1 st yr post-burn; same use 2 nd yr post- burn as unburned marshes	reed beds regrew by 2 nd yr; suggest that mid-March Rx of reeds inhibits breeding	ae
<u>Icterids</u> boat-tailed grackle	Chenier Plains, LA; brackish & salt marsh	2 winters	Exp	winter (Dec., early Jan.)	foraging	found immediately post burn, but not following yr	e	

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire * Type	Season of Fire	Use of Wetland	Response to Burns	Comments	
red-winged blackbird	Chenier Plains, LA; brackish & salt marsh	2 winters	Exp	winter (Dec., early Jan.)	foraging cover	found 2x more in burn following fire, 2 nd yr still lots of birds in burn	e	
icterids	Chenier Plains, LA; brackish & salt marsh	3 breeding seasons	Exp	winter (Dec., early Jan.)	nesting	NS, but 1.5 yr (2 nd yr) post-burn, more than 1 st or 3 rd yr	l	
red-winged blackbird	Chenier Plains, LA; brackish & salt marsh	3 breeding, 1 pre, 2 post	Exp	winter (Dec., early Jan.)	nesting	abundance increased in burned plots 1 st yr & then decrease 2 nd yr toward pre-burn	negatively correlated with % cover of dead veg & <i>S. patens</i>	f
boat-tailed grackle	Chenier Plains, LA; brackish & salt marsh	3 breeding, 1 pre, 2 post	Exp	winter (Dec., early Jan.)	nesting	abundance increased in burned plots 1 st yr & then decrease 2 nd yr toward pre-burn	negatively correlated with % cover of dead veg & <i>S. patens</i>	f
yellow-winged blackbird	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	only in unburned <i>Spartina</i> , similar abundance at end of study in <i>Juncus</i>	k	
icterids (residents)	Tall Timbers Research Station - Gannet Pond	4 mos.	Exp	winter	NA	more on burned shoreline except Red-wing blackbird	j	

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire * Type	Season of Fire	Use of Wetland	Response to Burns	Comments
blackbirds	Chenier Plains, LA; salt marsh	obs.	Exp	Fall	foraging	catching insects in smoke of fire	m
<u>Marsh Birds</u> "transients": snipe	Tall Timbers Research Station - Gannet Pond	4 mos.	Exp	winter		all had more on burned shoreline	j
Wilson's snipe	Rainwater Basin, NE; isolated wetland	2 wks pre-post of burn, 3 yrs of burns	Rx	spring		increased frequency & abundance in burn	burned adjacent to area surveyed n
jacksnipes & shorebirds	Chenier Plains, LA; salt marsh	obs.	Exp	Fall	NA	seen in burn	m
black rail (<i>Laterallus jamaicensis</i>)	St. Johns NWR, FL; (<i>Spartina bakeri</i>) marsh	obs.	Rx		NA	use unburned patches for refuge	mortality occurred in patches that subsequently burned o
Yuma clapper rail	Colorado River delta, CA & Mexico; cattail, reed, bulrush	1-6 yrs pre & 2-5 post burn	Rx,H	late winter- early spring	breeding foraging	more post- than pre- in burned areas, diminished over time	burns conducted shouldn't be large in spatial extent so birds have refugia p

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire Type	Season of Fire	Use of Wetland	Response to Burns	Comments
other rails & least bittern	Colorado River delta, CA & Mexico; cattail, reed, bulrush	1-6 yrs pre & 2-5 post burn	Rx,H	late winter-early spring	breeding foraging	no pre-post difference	p
Virginia rails	Colorado River delta, CA & Mexico; cattail, reed, bulrush	1-6 yrs pre & 2-5 post burn	Rx,H	late winter-early spring	breeding foraging	more post- than pre-burn	p
dot-winged crane	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	only in unburned <i>Spartina</i> ; not in burned <i>Juncus</i>	k
speckled crane	Pampas, Argentina; salt marsh	~1 yr	NA	spring	NA	only in unburned <i>Spartina</i>	k
<u>Waterfowl</u>							
Geese: snow, Canada, white-fronted	Chenier Plains, LA; salt marsh	obs.	Exp	Fall	foraging cover	increased abundance, 1939 burn: ~500k	note importance of spotty burns - no specific details provided
ducks	Chenier Plains, LA; salt marsh	obs.	Exp	Fall		thousands of ducks	m

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire * Type	Season of Fire	Use of Wetland	Response to Burns	Comments
geese	SE US wildlife refuges - freshwater tidal to coastal salt marsh	obs.	Rx	early fall, late winter	foraging	geese forage on green, succulent browse	q
blue geese (snow geese)	LA coastal marshes	obs.	NA	late Sept. to Jan.	foraging	heavy use	s
waterfowl	Sandhills, NE; isolated wetlands	obs., 2 yrs	Rx	winter		used during spring migration & for "movement & activities during the summer & fall"	r
ducks, other waterfowl	Delta Marsh, Manitoba; open sloughs & bays along lake	obs.	Rx	summer: after nesting; after end of July	nesting migration	burn more heavily used for nesting & autumn gatherings	t
ducks	Delta Marsh, Manitoba; open sloughs & bays along lake	obs.	W,H	April thru May	nesting	mortality of females, ducklings, destruction of nests	t
white geese	Chenier Plains, LA; brackish & salt marsh	2 winters	Exp	winter (Dec., early Jan.)	foraging	8 of 10 flocks in burn, other two elsewhere	e

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire * Type	Season of Fire	Use of Wetland	Response to Burns	Comments	
snow geese	Rainwater Basin, NE; isolated wetlands	2 wks pre-post of burn, 3 yrs of burns	Rx	spring	foraging	more abundant although in fewer burned wetlands		n
white-winged scoters	Mackenzie Delta, Canada; bogs & fens	1 summer (3 yrs post-fire)	W	NA, but likely summer	foraging nesting	scoter density higher with amphipod abundance	amphipods not related to fire; no nutrient effects 3 yrs post-fire	u
cackling & Pacific greater white-fronted geese	Fall River Valley, CA; wet meadow, could be riparian area	~2.5 mo. in spring post-burn, maybe 1 yr later on some plots	Rx	winter	foraging resting	on a couple days WF geese foraged exclusively in burned areas & were more numerous on these days	cackling geese did not visit experimental plots	v
ducks	south-central Canada; small isolated wetlands	2 breeding	Rx	spring & fall	breeding	occupancy not different between wetlands with burnt or unburnt edges		ab
coots	Grays Lake NWR, ID; fields on perimeter of montane wetland	2 yr pre & 2 yr post	Rx	fall	nesting	nest success declined, but was already declining pre-burn	nest success was already declining pre-burn	ac

Table 2-1. Continued

Species	Wetland Type	Length of Study	Fire Type *	Season of Fire	Use of Wetland	Response to Burns	Comments	
mottled duck	Chenier Plains, LA; brackish & salt marsh	2 breeding, 1 pre, 1 post	Exp	winter (mid- Jan.)	nesting	(artificial nest) high depredation, but no difference between yrs or trmts	veg cover 5 mo. post-burn similar to pre-burn, likely reason for no difference	^g
<u>Wading Birds</u>								
black-crowned night-heron, snowy egret, great blue heron	Bear River Migratory Bird Refuge, UT; impoundment	16 mo.	Rx	March	nesting	burn removes nesting substrate & nest materials	burned area compared to colonies, colonies not burned	^w
wading birds	Everglades - sawgrass (<i>Cladium jamaicense</i>)	obs.	W	late dry season	foraging nesting	no effect on colony, mortality of white ibis in slough		^x
wading birds (resident)	Tall Timbers Research Station - Gannet Pond	4 mo.	Exp	winter		all had more on burned shoreline		^j

^aLa Puma et al. 2007; ^bTaylor 1983; ^cBaker 1974; ^dGabrey & Afton 2000; ^eGabrey et al. 1999; ^fGabrey & Afton 2004; ^gGabrey et al. 2002; ^hAlmario et al. 2009; ⁱGabrey et al. 2001; ^jVogl 1973; ^kIsacch et al. 2004; ^lHanowski et al. 1999; ^mLynch 1941; ⁿBrennan et al. 2005; ^oLegare et al. 1998; ^pConway et al. 2010; ^qGivens 1962; ^rSchlichtemeier 1967; ^sPerkins 1968; ^tWard 1968; ^uHaszard & Clark 2007; ^vMcWilliams et al. 2007; ^wBray 1984; ^xEpanchin et al. 2002; ^yTucker & Robinson 2003; ^zMacleane et al. 2003; ^{aa}Wu & Zou 2011; ^{ab}Hochbaum et al. 1985; ^{ac}Austin & Buhl 2011; ^{ad}Zou et al. 2003; ^{ae}Hirano et al. 2003; ^{af}Vergeichik & Kozulin 2006; ^{ag}Kern et al. 2012

*Type of fire: Exp=experimental, H=human-caused, Rx=prescribed burn, W=wildfire

NA = not available

obs. = observational study

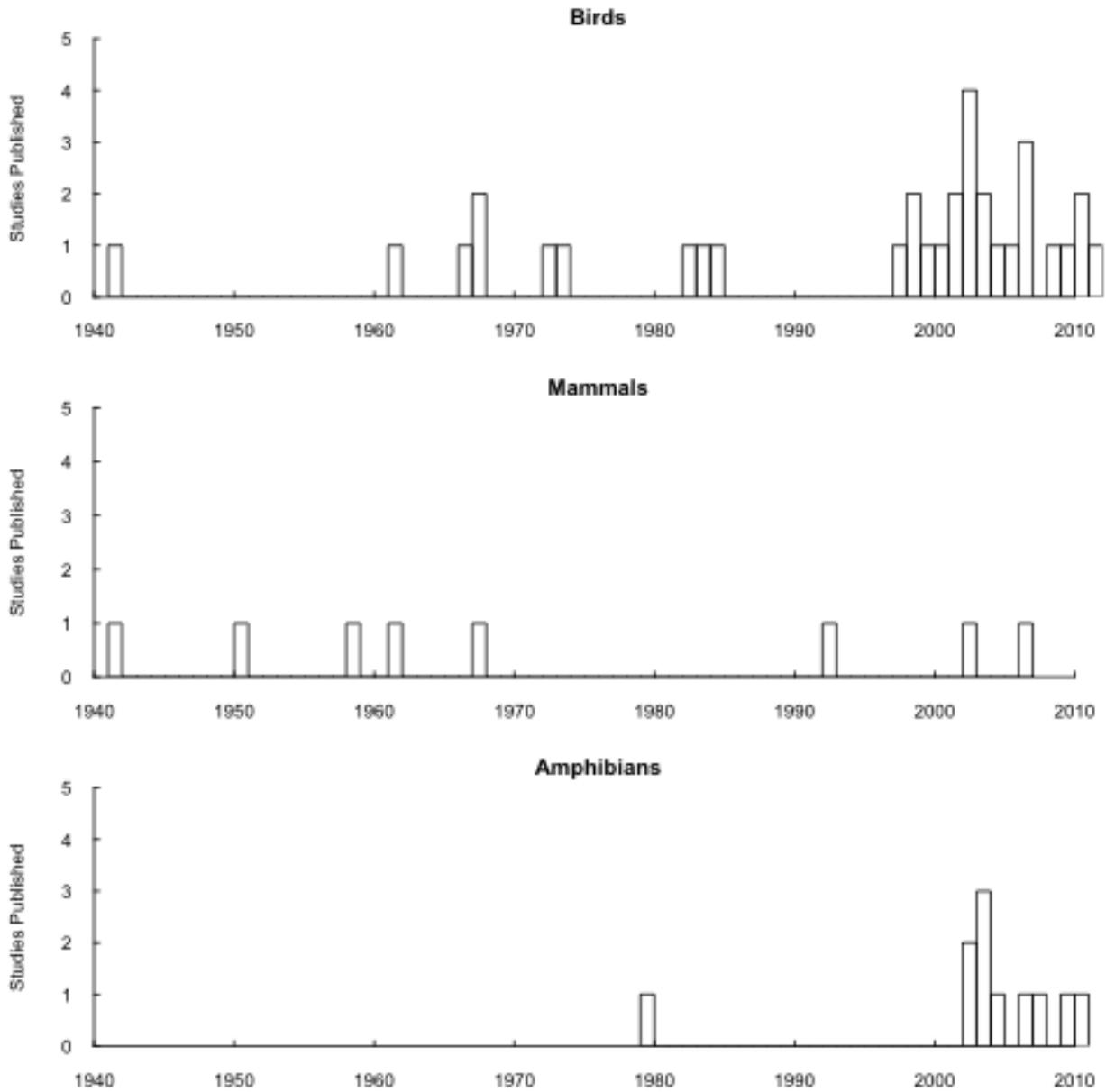


Figure 2-1. Number of studies per year of fire effects on each group in wetlands.

CHAPTER 3
EFFECTS OF PRESCRIBED FIRE ON FORAGING BY WADING BIRDS
(CICONIIFORMES) IN THE EVERGLADES

Introduction

Disturbance of upland areas via farm machinery, fire, and other physical disturbances often attract birds to forage or scavenge for displaced, injured, or recently killed prey (e.g., Komarek 1969, Smallwood et al. 1982, Tewes 1984, Toland 1987). The removal of vegetation can increase the availability of prey (Vickery et al. 2001) even when abundance or density of prey does not increase (Vickery et al. 2001, Munro et al. 2009). Thus, intake efficiency of birds may be increased because of improved availability of prey, but not due to abundance or diversity of prey (Devereux et al. 2006). Although changes in prey availability due to disturbance are known from upland habitats, it is unclear whether similar kinds of disturbance would result in the same effects on aquatic prey animals.

The absence of appropriate habitat and vegetative structure appears to strongly affect species specific responses to fire (Gabrey et al. 1999, Baldwin et al. 2007). Studies of responses of wetland birds to burns tend to record presence/absence of species after a burn, with many species not returning for a year or more (Venne, Chapter 2). For example, savannah sparrows tend to be found in areas with sparse vegetation within one year post-burn while sedge wrens prefer dense vegetation which has not burned in the previous two years (Baldwin et al. 2007). Fire may also positively affect foraging conditions for many wetland dependent birds. Recent burns appear to provide enhanced access to belowground plant parts for wintering geese (Gabrey et al. 1999) if burns are conducted during the appropriate time frame to make these resources available (Brennan et al. 2005, McWilliams et al. 2007). Fires also remove

dead plant litter and thus release nutrients. This process can increase nutritive value of vegetation (Smith et al. 1984), accessibility of food resources (Gabrey et al. 1999), and abundance of food resources such as invertebrates (de Szalay and Resh 1997).

Foraging success of long-legged wading birds (Ciconiiformes) depends largely on prey availability (Bancroft et al. 2002, Gawlik 2002). Water depth is a primary determinant of prey availability since wading birds are limited to foraging in water no deeper than their leg length (Powell 1987, Gawlik 2002). Emergent vegetation density also plays an integral role in prey availability in two important ways. Dense vegetation can impede access to prey, but may also increase prey density by improving cover to hide from predators. Thus, sparse vegetation may be preferred by wading birds compared to no or dense, emergent vegetation (Lantz et al. 2011), and edges may be preferred over open water (Stolen 2006).

Fire may affect foraging opportunities for wading birds through several mechanisms, including direct mortality of prey, alteration of habitat that prey depend on, increased primary production benefiting primary consumers through the release of nutrients and increased light, or changing accessibility of prey. Thus, burned areas should be attractive to wading birds for the duration of the effect resulting from fire. I tested the hypothesis that wading birds select for burned habitats over unburned habitat because burned areas in my study area (i.e., sawgrass ridges) are shallower than the surrounding marsh, vegetation is relatively sparse (making prey more accessible) compared to thick *Eleocharis* marshes, and prey densities are potentially greater than in similar unburned areas. I also predicted that wading birds in the Everglades would have a higher capture rate (captures per minute) and capture efficiency (captures per

attempt) in burned areas than in unburned areas, accounting for differences in water depth, flock size, and time since burn. Number of birds within a foraging flock affects foraging success of wading birds (Krebs 1974). I controlled for this variable because it could confound the analysis of fire effects on foraging success. Changes in vegetation and other factors associated with time since burn may also affect foraging success of wading birds, so I included time since burn as a covariate to describe the effect this variable has on foraging success of wading birds. I also tested the hypothesis that fires make prey available by injuring or killing prey during the burn, predicting that dead or injured prey would be more abundant in burned than unburned areas. Finally, I assumed that primary production post-burn would be elevated and predicted that prey densities would be greater in burned than unburned sawgrass.

Study Area

The Everglades is a large oligotrophic wetland in southern Florida, USA, where primary production is phosphorus-limited (Noe et al. 2001). Sawgrass (*Cladium jamaicense*) is the dominant vegetation, forming large elevated elongate “islands” (i.e., ridges) surrounded by open water sloughs and wet prairies dominated by sedges (*Eleocharis* spp.; Gunderson 1994). Rainfall occurs seasonally, primarily during the wet season from May to October resulting in strongly fluctuating water levels. Fire is a natural component of this landscape (Wade et al. 1980), occurring most frequently at the onset of the wet season (May – June) when lightning is common (Gunderson and Snyder 1994, Slocum et al. 2007). More acreage is burned during the transition from dry to wet season starting in May (when thunderstorms are prevalent and water depths are low) than at any other time of year and the greatest number of fires occurs at the peak of the seasonal thunderstorm pattern in July (Gunderson and Snyder 1994). Sawgrass

is a fire-adapted plant, growing quickly and recovering within 2 years post-burn (Wade et al. 1980). Furthermore, as sawgrass grows, the leaves spread away from the culm and senesce which helps promote fire, resulting in a wetland system that burns frequently (Gunderson and Snyder 1994). State and federal agencies conduct prescribed burns to mimic fire return intervals, although often not during the same season as natural fires. Moreover, prescribed burns are conducted to manage habitat for a variety of wildlife species and protect ecological features (e.g., tree islands) on the landscape from catastrophic fires. Prescribed fires generally are conducted in winter and spring when at least 10 cm of surface water protects the underlying peat layer. In contrast, wildfires that occur in dry years often burn the peat.

Methods

In 2009 and 2010, the Florida Fish and Wildlife Conservation Commission (FWC) conducted 3 burns each year in Water Conservation Area 3A of the Everglades that I used as treatments for effects of fire on foraging success of wading birds (Fig. 1). These burns ranged from 548 to 1039 ha and were composed of approximately 70-85% sawgrass (Table 1). All prescribed burns occurred within a six-week period from 15 February until 01 April. At the time of the burns, minimum estimated water depths ranged from 10 to 30.5 cm on the sawgrass ridges.

Prey Item Survey

During 2010, I surveyed 25 randomly selected locations in sawgrass in each burn unit for injured or dead biota that could serve as prey items for wading birds. I surveyed locations once pre-burn, and one day and one week post-burn. A set of random points (i.e., 50-100) was generated in ArcGIS within each burn border. Points landing in slough habitat were not used since sloughs do not burn. Points falling more than 200 meters

into the burn from the edge of the slough were also not used for safety concerns. At each location, I recorded water depth and maximum vegetation height, and two people searched within a 0.5 m radius for potential prey items pre-burn and injured or dead prey items post-burn. I searched in the water and among burned sawgrass culms, but did not count live fish since my presence disturbed these species.

Prey Density

I used two trapping techniques to sample aquatic prey within an approximately 884 ha prescribed burn and an area of similar size immediately adjacent to the prescribed burn. The prescribed burn was conducted on 02 March 2011 in Water Conservation Area 3AS (Fig. 1). Minimum water depths were 15-20 cm at the time of burn. I generated random points within the sawgrass area of the burn unit and in an adjacent unburned area. The unburned sawgrass was east and adjacent to the prescribed burn. Starting one day post-burn, I measured small fish and macroinvertebrate density and environmental characteristics at the random points in burned and unburned sawgrass ridges with 1-m² aluminum-sided throw traps and Gee minnow traps (23 x 45 cm, 3.2 mm mesh, Memphis Net & Twine Co., Inc., Memphis, TN). I threw three throw traps in each sampling location and removed vegetation to facilitate clearing of traps. I cleared all traps with bar seine and dip net following methods of Jordan et al. (1997a) and preserved all aquatic organisms that were ≥ 5 mm in length. Within each throw trap, I measured water depth, vegetation height, estimated percent periphyton cover to the nearest 5%, and counted sawgrass stems. At each sampling location with adequate water depths (≥ 10 cm), I set 3 Gee minnow traps (23 x 45 cm, 3.2 mm mesh) for 2 hours. After 2 hours, I collected and preserved all aquatic organisms captured. Organisms that were too large for the collection vials were measured in the field and

released. All organisms were identified to species and measured (standard length (SL) for fish and snout:vent length (SVL) for amphibians) to the nearest mm.

Foraging Observations

I observed foraging great egrets (*Ardea alba*) in burned sawgrass and sloughs adjoining burned sawgrass (hereafter termed “sloughs adjacent to burns”) using a 6.5 m tower mounted on an airboat. I selected individuals for observations that were foraging either singly or in groups and would be visible (i.e., not readily obstructed by vegetation or other wading birds) for much of the observation period. I usually observed individual birds for 5 min, though some observations were as long as 15 min. I accepted observations of less than 5 min duration if my view of the bird was obstructed by vegetation or the bird flew away. I counted the number of attempts to capture prey and number of successful attempts each bird made. I recorded number of individuals of each species in a flock. When observing a flock, I observed as many birds in each flock as possible until the birds flew away or I could no longer ensure I was observing an identifiable new bird. After observations were completed, I recorded water depth and coordinates at the foraging location.

Foraging Habitat Selection

In 2009 and 2010, I set up aerial survey transects (8 transects in 2009 and 5 in 2010) to cover 100% of the three burn units in each year and an equivalent adjacent area at the same latitude that would remain unburned (Fig. 1). Transects were oriented east-west and separated by 1.33 km. Areas were surveyed weekly for 8-10 weeks until the sloughs dried or the wading birds dispersed. I flew with a second observer looking out the opposite side of a fixed-wing Cessna 182 on transects at 244 m (800 ft) at 185-222 km/h (100-120 knots). We recorded species, number of individuals, and habitat in

which white foraging wading birds were observed on our side of the plane. Habitat categories were sawgrass, burned sawgrass, slough, sloughs adjacent to burns, and track (i.e., trails created by airboats). When groups of birds were >6, the observer would take one or more photos of the group to be counted later by two observers. Birds were categorized to species when possible. If they could not be identified to species, I categorized them as white wader or small blue heron. Groups were individually numbered so that if they overlapped habitats, they could be identified as a distinct unit.

I digitized burned areas using Digital Orthophoto Quarter Quads (DOQQs) from 2003 in ArcGIS (Esri, Redlands, CA) based on photographs of the burn taken during flights from 305-610 m altitude. Area of each digitized patch was calculated for each burn. I digitized airboat track length within each survey area using files provided by FWC and DOQQs and calculated airboat track area by multiplying length by 2 m (approximate airboat width). Then, I clipped vegetation types using the vegetation data in Rutchey et al. (2005) in my survey areas and burn units (to determine area of sloughs adjacent to burns). I subtracted airboat track area (approximated to be 80% through grass and 20% through slough) from grass and slough since burned areas were digitized to exclude tracks. I reduced vegetation types from Rutchey et al. (2005) to my categories, and calculated area of each habitat category for each week surveyed: burn, grass, tree island, slough, sloughs adjacent to burns, and airboat track. I used water depth data over the period of aerial surveys at gaging station 3A-S_B to show water level trends within the study area (SFWMD 2012). Water levels are reported relative to NGVD29.

Statistical Analysis - Prey

Due to the low number of potential prey items found, no statistical analyses were performed on data collected during the prey item survey. From samples collected with a 1-m² throw trap, I checked normality of environmental variables (i.e., water depth, sawgrass stem and total stem density, vegetation height, and % periphyton and vegetation cover), density of aquatic organisms (i.e., fish, crayfish (*Procambarus* spp.), grass shrimp (*Palaemonetes paludosa*), amphibians, and aquatic invertebrates (>5 mm total length)), and length of aquatic organisms (fish and crayfish). I also checked normality of length of fish and abundance of fish, crayfish, and amphibians caught in minnow traps. All environmental variables, crayfish density and length in throw traps and fish standard length in minnow traps and square-root transformed aquatic invertebrate density were normal and tested with a two-sample t-test for differences between burned and unburned sawgrass. All other variables of aquatic organisms in throw and minnow traps could not be normalized and I used a Kruskal-Wallis rank sum test to test for differences between burned and unburned sawgrass.

Statistical Analysis – Foraging Observations

I constructed models of capture rate (number of captures per min) and capture efficiency (number of captures per attempt) for great egrets *a priori*. Models of capture rate were generalized linear models with a gamma distribution using a log-link function. I added 0.01 to capture rate in all models because there were zero values in capture rate. Models of capture efficiency were generalized linear models with a quasibinomial distribution due to response type and number of zeroes in the data set. Models were constructed using a combination of water depth (linear or quadratic term), flock size, flock composition (single vs. mixed species), days since burn, habitat (burn vs. sloughs

adjacent to burns), and year. I selected models of capture rate using the corrected Akaike's Information Criterion (AIC_c) and of capture efficiency using corrected QAIC ($QAIC_c$; Burnham and Anderson 2002). I rescaled AIC values (Δ_i) based on the AIC value of the best model (i.e., lowest AIC value), and calculated weighted values (w_i). I reported coefficients for all models with $\Delta_i < 2$. Percent deviation (%D) was calculated from the null and residual deviances (i.e., $\%D = (\text{null-residual})/\text{null}$) for models of capture rate and capture efficiency.

Statistical Analysis – Foraging Habitat Selection

I calculated habitat selection ratios $[(\text{number of birds in each habitat per survey}) / \text{total number of birds per survey}] / (\text{amount of each habitat per survey} / \text{total amount of habitat per survey})$ for each year following Manly et al. (2002). A selection ratio of 1 represents use of the habitat equal to its availability. Selection ratios < 1 indicate avoidance while selection ratios > 1 indicate selection for the habitat. I compared ratios in each habitat type to expected use via a Chi-squared analysis and calculated 95% confidence limits using the Bonferroni correction. All statistical analyses were performed using R 2.10.1 (R Development Core Team 2009).

Results

Foraging Habitat Selection

Great egrets had a high selection ratio (showing selection) for burns in the first 2 weeks (approximately 3.5 weeks after the first burn) of the surveys in 2009 (Fig. 3-2, Table 3-2). In 2010, great egrets similarly selected for burns for approximately 3 weeks after the first prescribed burn (Fig. 3-3, Table 3-3). In some habitat types, great egrets were not observed during surveys and no data point is included (Fig. 3-3). Great egrets avoided burns when there was no standing water in the burn. Great egrets only selected

for burns in proportion to the availability of burned areas in the survey area immediately after an additional prescribed burn in 2009 and for the last four surveys in 2010 (Tables 3-2 & 3-3). Conversely, great egrets strongly avoided unburned sawgrass in both years (Tables 3-2 & 3-3). Much of the use of unburned grass by great egrets occurred in thin strips of sawgrass in the edge between burn and sloughs adjacent to burns. In 2009, the selection ratio for sloughs adjacent to burns increased as water levels declined (Fig. 3-2, Table 3-2). To account for potential differences in water depths between sloughs, I compared great egret use of slough and sloughs adjacent to burns. Great egrets selected for both categories of slough equal to or more than their availability across all surveys (Tables 3-2 & 3-3). Two exceptions occurred in 2009 when great egrets avoided sloughs adjacent to burns in mid-March and in the week after a new prescribed burn when great egrets selected for sloughs adjacent to burns and avoided sloughs even as water levels were dropping and ridge habitats were not available (Fig. 3-2). Great egrets used airboat tracks more than available (Figs. 3-2 & 3-3), especially in conjunction with a sharp increase in water levels, likely because tracks are typically deeper water than the surrounding sloughs.

White ibis selected for burns in both years (particularly strongly in 2010), but avoided burns once water levels in burned areas were at or below the soil surface of the burned area (Tables 3-4 & 3-5, Figs. 3-4 & 3-5). In some habitat types, white ibis were not observed during surveys and no data point is included (Fig. 3-5). Conversely, white ibis strongly avoided unburned sawgrass stands in both years (Tables 3-4 & 3-5). Comparing white ibis use of sloughs adjacent to burns and slough in 2009, white ibis selected for sloughs adjacent to burns more than their availability and selected for

sloughs about equal to their availability in the survey area (Table 3-4 & 3-5). In the week following the final prescribed burn in 2009 as water levels were receding, white ibis selected for sloughs adjacent to burns and avoided sloughs (Table 3-4, Fig. 3-4). To account for potential differences in water depth, I compared white ibis use of sloughs adjacent to burns and slough. White ibis selected for sloughs adjacent to burns and slough much more than they were available in 2010, except for one survey in mid-April where it appears that ibis were selecting for burns (Fig. 3-5). Ibis strongly selected for airboat tracks in 2009 when water levels had receded the most, but only briefly used airboat tracks in 2010 when water levels were dropping (Figs. 3-4 & 3-5).

Foraging Observations

I observed a total of 104 foraging great egrets in 2009 and 2010. Capture rate of great egrets ranged from 0-3.2 per min with a mean of 0.43 per min across both years and all foraging locations. Capture rates in 2009 in sloughs adjacent to burns were higher than in sloughs and other Everglades habitats in which capture rates have been previously quantified (Table 3-6). Water depths at foraging locations were deeper in 2010 than 2009 in sloughs adjacent to burns (Table 3-7). In 2009, water levels receded during the sampling period, to the point that no surface water was available in the study area and no foraging was observed after 12 April. However, in 2010, while water levels initially declined, they rose again in early March and remained fairly steady until the end of observations on 30 March.

The best model of great egret capture rate included flock size, days since burn, habitat, water depth, and flock composition (Table 3-8). Percent deviance of the best model was 26.9%. Great egret capture rate was greater in sloughs adjacent to burns than in burned sawgrass (Table 3-9). Water depth was positively related to capture rate,

however, there was also an interaction between depth and habitat that was negatively related to capture rate. Capture rate did not differ with depth in burns, but was negatively related to water depth in sloughs adjacent to burns. Days since burn was positively related to capture rate. In other words, capture rate of great egrets increased with time after the burn occurred. Great egrets foraging in conspecific-only flocks had a higher capture rate than in multi-specific flocks, but capture rate also declined as flock size grew. Effect size for water depth and flock size was very small indicating minimal contribution to the model (Table 3-9) and thus are not considered driving factors of capture rate.

Capture efficiency (captures/strike) of great egrets ranged from 0-1 with a mean of 0.39 captures per attempt (Table 3-7). Capture efficiencies of this study fell within the range of other studies of great egrets (Table 3-6). The models that best explained capture efficiency included flock size, flock composition, habitat, days since burn, and water depth (Table 3-10). One of the top two models ($\Delta QAIC_c < 2$) included an interaction between depth and habitat, however the $\Delta QAIC_c$ value was approximately 2, indicating that the additional variable did not change the likelihood of the model, but increased the $\Delta QAIC_c$ by the penalty term of 2 imposed by AIC for each additional variable in the model. Percent deviance of both models was approximately 15.8%. Water depth, foraging in conspecific flocks, and flock size were positively related to capture efficiency, however, effect size for water depth and flock size was very small, indicating minimal contribution of these variables to the models (Table 3-9). Capture efficiency decreased with days since burn in sloughs adjacent to burns.

Prey Item Survey

I conducted a single pre-burn survey two to four weeks prior to each of two prescribed burns, and two sets of post-burn surveys (1 day and 1 week post-burn) on three prescribed burns. In pre-burn surveys, I found six possible prey items, all spiders, at 6 of 50 points (0.15 items/m²). Mean water depths pre-burn were 8.5 cm in Berg burn and 14.5 cm in the 9.5 West burn with water depths at individual sampling locations ranging from 0-22 cm. Surveys immediately after the burn (1 day post-burn) yielded 9 prey items at 7 of 75 points (0.12 items/m²). Dead prey included one snail and two millipedes and live prey items included three spiders, two unidentified invertebrates, and one snail. Similarly, surveys one week after the burn yielded 13 potential prey items (0.22 items/m²; three worms and two millipedes within a sawgrass culm, five spiders, one unidentified invertebrates, and two snails: one live, one dead). Mean water depths ranged from 6.9-24.3 cm post-burn with a range of 0-31 cm at individual sampling locations. Most of these invertebrates are unlikely to be actual prey items sufficient to cause wading birds to forage in a recent burn because they were small, hidden in sawgrass, and scarce.

Prey Density

Most sampling locations were within 10 m of the edge of the slough because water depth often was too shallow for sampling farther into the sawgrass stand. Water depths in sampled locations were about 5 cm deeper in unburned than burned sawgrass (Table 3-11), suggesting that I inadvertently selected deeper water locations to sample unburned sawgrass despite selecting areas immediately adjacent to the burn that should have similar water depths. Stem density was significantly different, likely because stems of small plants (e.g., *Eleocharis* sp.) in burned areas were consumed

entirely by fire and were not present to be counted. Percent cover of vegetation and periphyton were significantly greater in unburned sawgrass. Density and sizes of most potential prey items did not differ between burned sawgrass ridges and unburned sawgrass (Table 3-11). Amphibians (Peninsula newt (*Notophthalmus viridescens piaropicola*), siren (*Siren lacertina*), tadpoles, and adult Florida cricket frog (*Acris gryllus dorsalis*)) were at a significantly higher density in burns than unburned sawgrass in throw trap samples. Density of aquatic invertebrates (identified to lowest taxa possible: Belastomatid, Dysticid, Hirudinea, Odonata, Oligochaeta, and *Pelocoris femoratus* (alligator flea)) did not differ among treatments.

Discussion

Wading birds selected recently burned areas for a number of weeks post-burn in greater proportion than was available. The removal of above water vegetation by fire exposed these sawgrass ridges, which are shallower in water depth than the surrounding sloughs (Loveless 1959). Sawgrass on these ridges grows in dense, tall (mean: 0.8-1.5 m, but up to 3 m) stands (Gunderson 1994) that can inhibit movement and visibility by large animals such as wading birds. Through the removal of sawgrass by fire, this obstruction was eliminated, permitting wading bird access to these areas. Sawgrass starts growing almost immediately after a fire, resulting in changing vegetation conditions on burned ridges. While vegetation height increased, it is unlikely over the duration of this study that wading birds avoided burned areas because of the increasing vegetation heights. Shallow water depths are preferred by foraging wading birds given similar prey densities between accessible shallow and deep water habitats (Gawlik 2002) and depth may be what primarily attracts birds to these recently burned areas. Not only did wading birds show a preference for burned areas, but they also

remained in these areas over multiple weeks while water levels dropped and prey populations were depleted through foraging by wading birds and migration of prey to deeper water refuges. Field observations provide evidence that wading birds quit foraging in burned areas when water levels dropped below the marsh surface.

One of my hypotheses was that wading birds are attracted to recently burned areas because of prey items injured or killed by the fire. I found almost no such potential prey items post-burn, which were at levels insufficient to result in wading birds selecting burned areas over sloughs. The lack of potential prey items post-burn is not surprising given the low density of potential prey items found pre-burn. Burns in upland areas similarly yield few dead prey resources after the burn. Instead, many small mammals, insects, and other potential prey frequently flee the flame front, and are targeted during the fire by aerial and ground predators such as hawks, kestrels, and cattle egrets (Komarek 1969, Smallwood et al. 1982, Tewes 1984).

Fish densities in burned and unburned sawgrass did not differ, indicating that burning did not affect fish density in sawgrass. The densities in this study were typically lower than densities in sloughs in the Everglades (Loftus and Eklund 1994, Jordan 1996, Jordan et al. 1997b, Trexler et al. 2002, Williams and Trexler 2006). Jordan (1996) found lower densities of fish in sawgrass than in sloughs. While water depths were shallower in this study than in other studies of fish density, the values of fish density in this study were similar to a location sampled by Trexler et al. (2005) that also had shallow water depths. I was forced by low water levels to collect the majority of samples near the edge of the ridge due to shallow water levels farther onto the ridge, which may have biased measures of density or assemblage composition. However,

these samples are representative of the fish available to wading birds foraging in areas of burned sawgrass just before the burns have no standing water. Thus, while fish densities were not very high in burned areas relative to the sloughs, fish are available to foraging wading birds.

Capture rate of great egrets was much higher in sloughs adjacent to burns than in burned areas. Capture rates in this study fell in the range observed in other areas of the Everglades (Surdick 1998, Sizemore 2009, Lantz et al. 2010, 2011) although capture rates in 2010 were at the low end of those reported. Fast prey capture rates may indicate that birds spend less time foraging to meet their energetic requirements, however, this metric gives no indication of the quality of the prey being captured or the quantity of prey available. For example, larger prey (e.g., siren) may require more handling time than small prey (e.g., small fish) although the caloric intake of large prey is typically much greater than a number of small prey captured in rapid succession. Given that capture rates were higher in sloughs adjacent to burns, it seems contrary to expectations that great egrets preferentially foraged in burned areas. However, sloughs are deeper water habitats than burned sawgrass and at the time that burns were available, many sloughs adjacent to burns may have had water levels deeper than appropriate for great egrets. While I observed foraging wading birds in an overlapping range of water depths in both habitat types, water depths in sloughs adjacent to burns where some great egrets foraged were at the upper limit of water depths in which wading birds can forage and may have limited the inclusion of birds foraging in deep water habitats (Powell 1987, Gawlik 2002).

Overall, capture efficiency was greater in burns than in sloughs adjacent to burns despite lower prey densities. As with capture rate, mean values of capture efficiency were in the range of other capture efficiencies reported for great egrets foraging in the Everglades (Surdick 1998, Sizemore 2009, Lantz et al. 2010, 2011). Greater capture efficiency in burned areas than sloughs adjacent to burns is compatible with the prediction that wading birds select burned ridges over sloughs. Burned areas have less submerged aquatic vegetation and almost no thick periphyton mat (pers. obs., Venne) within the water column, unlike sloughs. This provides less cover for fish and may enhance the ability of predators to see and capture prey.

Burned sawgrass ridges provide shallow areas that wading birds appear to prefer more than sloughs that have deeper water and typically have higher prey densities. I found no evidence that the few potential prey items that were killed by the fire were sufficient to cause wading birds to select these areas for the purpose of scavenging. Wading birds appear to be selecting shallow water habitats despite lower capture rate. Habitat rather than foraging conditions may influence habitat selection (Gawlik 2002, Lantz et al. 2010, 2011), which would explain why wading birds selected burned areas. While prescribed burns are a small percentage of the Everglades ecosystem, the removal of the sawgrass canopy by these burns provides shallow water habitats in which wading birds can forage efficiently, albeit not at a fast rate. Regardless, wading birds must capture prey of sufficient caloric value while foraging. Prescribed fires are typically conducted during the dry season when water levels are dropping. Wading birds may have a limited window of opportunity to forage on burned ridges when water depths

are appropriate and before vegetation grows too tall. Fires conducted at another time of year may yield different results and should be explored.

Table 3-1. Description of prescribed burns conducted by the Florida Fish and Wildlife Conservation Commission in Water Conservation Area 3A used for wading bird foraging observations and/or prey studies in 2009 – 2011.

Burn ^a	HeatNSmoaks ^b	Jessie's Holiday ^b	Lost Lemon ^b	Hackberry ^{b,c}	Berg ^{b,c}	9.5 West ^c	Apple Camp ^d
Date burned	17 Feb. 09	26 Feb. 09	27 Mar. 09	16 Feb. 10	03 Mar. 10	01 Apr. 10	02 Mar. 11
Size (ha)	1003	931	1039	817	548	690	884
Last Yr Burned ^e	2004	2005	2005-W	2007-E	2006	1997-N 2006-W	2005
<i>Estimated % Habitat Composition</i>							
Sawgrass	70	70	85	70	75	70	67
Slough	14	19	7	29	13	25	15
Other	16	11	8	1	12	5	18
<i>Fuel Density (%)</i>							
Light	30	30	20	40	20	20	15
Moderate	50	55	70	40	25	35	15
Heavy	20	15	10	10	55	45	70
<i>Weather Conditions</i>							
Dispersion	45	62	70	60	48	42	55
Min. Mixing Ht	3000	4000	5000	2700	2700	--	4000
<i>Onsite Conditions</i>							
Time Taken	10:55	10:10	11:10	12:00	9:00	9:50	10:49
Wind	NE 5/9	NE 6/9	SE 9/16	NW 7	W 5.3/8.9	NE 1.2/3.1	NE 11
RH (%)	60	61	62	52	75	80	60
Air Temp.	72	75	81	64	55	67	80
Flame Length (ft)	7		8-10	4-10			3-15
ROS				2 ft/min			

^aData taken from burn prescriptions provided by FWC. These are estimated percent habitat compositions.

^bBurn used for wading bird foraging observations.

^cBurn used for pre- and post-burn prey quantification.

^dBurn used for comparison of prey densities.

^eW, E, and N designates burn occurred in west, east, and north, respectively, portion of burn unit in year listed.

Table 3-2. Great egret habitat selection ratio (Bonferroni adjusted 95% confidence interval) for 2009.

Survey Date	Slough adj. Burn ^a	Burn	Grass	Slough	Track
Feb. 28	0.718 (0.18-1.26) ^{ns}	2.985 (2.03-3.94)	0.265 (0.13-0.40)	1.019 (0.75-1.29) ^{ns}	54.44 (34.84-74.04)
Mar. 06	0.761 (0.36-1.17) ^{ns}	3.200 (2.49-3.91)	0.262 (0.16-0.36)	1.273 (1.07-1.48) ^{ns}	28.16 (17.22-39.09)
Mar. 12	2.217 (1.75-2.68)	1.934 (1.51-2.36)	0.052 (0.03-0.08)	1.866 (1.75-1.98)	24.22 (17.83-30.60)
Mar. 20	0.712 (0.50-0.93) ^{ns}	0.407 (0.25-0.57)	0.024 (0.01-0.04)	2.191 (2.09-2.29)	41.16 (34.20-48.11)
Mar. 28	2.274 (1.78-2.77)	0.753 (0.49-1.02) ^{ns}	0.019 (0.00-0.04)	1.764 (1.60-1.93)	43.83 (33.04-54.63)
Apr. 03	4.080 (3.67-4.49)	0.230 (0.13-0.33)	0.041 (0.02-0.06)	1.346 (1.23-1.46)	51.21 (43.36-59.06)
Apr. 10	0.935 (0.75-1.12) ^{ns}	0.005 (0.00-0.02)	0.016 (0.01-0.03)	2.624 (2.55-2.70)	24.25 (19.65-28.85)

^{ns}Chi-square p-value >0.05 for test of habitat selection different than expected

^aThis is sloughs adjacent to burns.

Table 3-3. Great egret habitat selection ratio (Bonferroni adjusted 95% confidence interval) for 2010.

Week	Slough adj. Burn ^a	Burn	Grass	Slough	Track
Feb. 15	NA	NA	0.154 (0.05-0.26)	2.434 (2.16-2.71)	20.99 (6.77-32.21)
Feb. 26	1.486 (0.53-2.44) ^{ns}	1.775 (0.77-2.78) ^{ns}	0.540 (0.41-0.67)	1.830 (1.55-2.11)	1.673 (0.00-4.71) ^{ns}
Mar. 05	2.095 (1.45-2.74)	2.898 (2.30-3.50)	0.479 (0.39-0.57)	1.249 (1.04-1.46) ^{ns}	4.366 (0.85-7.88)
Mar. 13	2.401 (1.60-3.20)	0.543 (0.20-0.89) ^{ns}	0.253 (0.17-0.34)	2.325 (2.07-2.58)	8.977 (3.14-14.82)
Mar. 19	3.213 (2.25-4.17)	0.386 (0.08-0.67) ^{ns}	0.046 (0.00-0.09)	2.644 (2.39-2.90)	8.167 (2.21-14.12)
Mar. 25	2.349 (1.45-3.25)	0 ^b	0.026 (0.00-0.06)	2.989 (2.75-3.22)	9.188 (2.51-15.87)
Mar. 31	2.394 (1.39-3.40)	0.971 (0.41-1.54) ^{ns}	0.120 (0.04-0.20)	1.899 (1.57-2.23)	40.89 (26.49-55.29)
Apr. 08	2.836 (1.99-3.68)	0.868 (0.42-1.32) ^{ns}	0.063 (0.00-0.12)	2.385 (2.01-2.76)	7.934 (0.85-15.02)
Apr. 15	2.747 (1.90-3.59)	0.768 (0.34-1.20) ^{ns}	0.064 (0.00-0.13)	2.463 (2.09-2.84)	8.127 (0.87-15.38)
Apr. 25	2.486 (1.42-3.55)	1.155 (0.49-1.82) ^{ns}	0.185 (0.05-0.32)	2.122 (1.63-2.62)	6.828 (0.00-15.48)

^{ns}Chi-square p-value >0.05 for test of habitat selection different than expected

NA=not available, this survey occurred pre-burn.

^aThis is sloughs adjacent to burns.

^bSelection ratios of zero indicate that no birds were observed in this habitat.

Table 3-4. White ibis habitat selection ratio (Bonferroni adjusted 95% confidence interval) for 2009.

Survey Date	Slough adj. Burn ^a	Burn	Grass	Slough	Track
Feb. 28	2.567 (1.97-3.17)	3.476 (2.83-4.12)	0.235 (0.15-0.32)	1.123 (0.94-1.30) ^{ns}	0 ^b
Mar. 06	2.165 (1.77-2.56)	1.801 (1.45-2.16)	0.432 (0.36-0.51)	1.365 (1.24-1.49)	2.737 (0.52-4.95) ^{ns}
Mar. 12	3.071 (2.74-3.40)	1.979 (1.71-2.25)	0.097 (0.08-0.12)	1.795 (1.72-1.87)	9.960 (7.33-12.59)
Mar. 20	0.591 (0.43-0.75)	0.544 (0.40-0.69)	0.217 (0.18-0.26)	2.259 (2.18-2.34)	13.32 (9.88-16.76)
Mar. 28	1.417 (1.13-1.71)	1.792 (1.52-2.06)	0.008 (0.00-0.02)	1.920 (1.80-2.04)	19.70 (14.34-25.07)
Apr. 03	6.151 (5.67-6.64)	0 ^b	0.050 (0.02-0.08)	0.855 (0.74-0.97) ^{ns}	51.14 (42.27-60.00)
Apr. 10	2.231 (1.89-2.57)	0 ^b	0.013 (0.00-0.03)	2.462 (2.36-2.56)	8.456 (4.93-11.98)

^{ns}Chi-square p-value >0.05 for test of habitat selection different than expected

^aThis is sloughs adjacent to burns.

^bSelection ratios of zero indicate that no birds were observed in this habitat.

Table 3-5. White ibis habitat selection ratio (Bonferroni adjusted 95% confidence interval) for 2010.

Survey Date	Slough adj. Burn ^a	Burn	Grass	Slough	Track
Feb. 15	NA	NA	0.271 (0.13-0.41)	2.428 (2.13-2.73)	5.529 (0.00-13.64) ^{ns}
Feb. 26	6.443 (5.26-7.62)	5.159 (4.11-6.21)	0.264 (0.20-0.33)	1.226 (1.04-1.41) ^{ns}	0.745 (0.00-2.10) ^{ns}
Mar. 05	1.168 (0.92-1.41) ^{ns}	5.410 (5.07-5.75)	0.099 (0.08-0.12)	1.553 (1.45-1.66)	0 ^b
Mar. 13	2.156 (1.51-2.80)	2.416 (1.86-2.97)	0.011 (0.00-0.03)	2.464 (2.26-2.67)	0 ^b
Mar. 19	2.774 (1.96-3.59)	0.563 (0.23-0.90) ^{ns}	0.070 (0.02-0.12)	2.785 (2.57-3.00)	0 ^b
Mar. 25	0 ^b	0.192 (0.00-0.47) ^{ns}	0.048 (0.00-0.10)	3.584 (3.44-3.73)	0 ^b
Mar. 31	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b
Apr. 08	4.061 (0.00-8.84) ^{ns}	5.179 (1.53-8.83)	0 ^b	0 ^b	0 ^b
Apr. 15	0.241 (0.00-0.85) ^{ns}	7.182 (6.10-8.26)	0.083 (0.00-0.23)	0.283 (0.00-0.69) ^{ns}	0 ^b
Apr. 25	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b

^{ns}Chi-square p-value >0.05 for test of habitat selection different than expected

NA=not available, this survey occurred pre-burn.

^aThis is sloughs adjacent to burns.

^bSelection ratios of zero indicate that no birds were observed in this habitat.

Table 3-6. Capture rates (captures per minute) and capture efficiencies (captures per attempt) reported for the great egret (*Ardea alba*) in southern Florida marshes.

Study	Year or Condition	Capture Rate (N)	Capture Efficiency (N)	Location
Surdick (1998)	1996	0.4 (292)	NA	Everglades
	1997	0.2 (593)	NA	
Sizemore (2009)	2008	0.46 (82)	0.60 (76)	Agricultural fields
	2009	0.34 (130)	0.47 (115)	
Lantz et al. (2010)	Jan. shallow	0.19-0.29 (35)	0.30-0.60 (29)	SAV ^a density experiment
	Jan. deep	0.26-1.58 (19)	0.56-1.0 (16)	
	Apr. shallow	0.23-0.75 (12)	0.33-0.75 (11)	
Lantz et al. (2011)	2008	0-0.66 (12)	0.13-0.34 (11)	Emergent vegetation experiment
This study	2009	0.59 (60)	0.40 (60)	Everglades WCA-3A
	2010	0.18 (38)	0.35 (38)	

^aSAV is submerged aquatic vegetation

Table 3-7. Capture rates (captures per minute) and capture efficiencies (captures per attempt) of great egret (*Ardea alba*) in 2009 and 2010 in Water Conservation Area 3A of the Everglades, USA.

Variable	2009		2010	
	Burn	Slough adj. Burn ^a	Burn	Slough adj. Burn ^a
Number of observations	17	43	14	24
Mean Capture Rate (\pm sd)	0.30 (0.3)	0.71 (0.9)	0.07 (0.1)	0.24 (0.2)
Range of Capture Rate	0-0.9	0-3.2	0-0.4	0-0.8
Mean Capture Efficiency (\pm sd)	0.46 (0.4)	0.38 (0.3)	0.18 (0.3)	0.45 (0.4)
Range of Capture Efficiency	0-1	0-1	0-1	0-1
Mean Attempts per minute	0.6 (0.5)	1.3 (1.2)	0.3 (0.3)	0.5 (0.4)
Water depth (cm)	12.1 (8.9)	16.5 (4.6)	13.9 (4.9)	22.7 (4.4)
Range of water depth (cm)	0-21	8-25	7-21	14-30

^aSloughs adjacent to burns

Table 3-8. Candidate set of models of great egret capture rate using corrected Akaike's Information Criterion (AICc) to select generalized linear models constructed with environmental characteristics in foraging locations in Water Conservation Area 3A of the Everglades, USA, 2009 and 2010.

Model	Model Variables ^a	k ^b	Δ_i	w _i
m5a	D, FS, FC, Hab, dSB, D*Hab	8	0.0	0.768
m18a	D2, FS, FC, dSB, Hab, D2*Hab	8	4.5	0.081
m5	D, FS, Hab, dSB	6	4.9	0.066
m20	Yr, FS, FC, Hab, dSB	7	5.6	0.046
m18	D2, FS, FC, Hab, dSB	7	7.0	0.023
m4	D, FS, Hab	5	9.7	0.006
m7	FS, Hab	4	10.6	0.004
m17	D2, FS, FC, Hab	6	10.9	0.003
m11	FS, FC, Hab, dSB	6	12.2	0.002
m10	FS, FC, Hab, dSB	5	12.8	0.001
m00	Yr, Hab, dSB	5	18.0	< 0.001
m001	D, Hab, Hab*D	5	19.2	< 0.001
m9	FS, dSB	4	20.4	< 0.001
m16	D2, FS, FC	5	23.2	< 0.001
m6	FS	3	24.2	< 0.001
m3	D, FS, FC	5	24.6	< 0.001
m19	Yr	3	25.2	< 0.001
m8	FS, FC	4	25.9	< 0.001
m2	D, Hab	4	28.1	< 0.001
m13	Hab, dSB	4	31.1	< 0.001
m12	Hab	3	31.1	< 0.001
m15	D2	3	34.3	< 0.001
m1	D	3	34.7	< 0.001
m14	dSB	3	35.0	< 0.001

^aD = depth, D2 = depth squared, dSB = days since burned, FC = flock composition, FS = flock size, Hab = habitat bird was foraging in, Yr = year, D*Hab = interaction of depth and habitat, D2*Hab = interaction of depth squared and habitat

^bNumber of parameters included within the model

Table 3-9. Coefficients of generalized linear models of great egret capture rate (Rate) selected using corrected Akaike's Information Criteria (AIC_c) and capture efficiency (Efficiency) selected using corrected quasi-AIC (QAIC_c). Models of capture rate use a gamma distribution and capture efficiency use a quasibinomial distribution.

Variable				<u>Flock Comp</u>	<u>Habitat</u>			
	Intercept	Depth	Flock Size	Single spp.	BSL ^a	dSB ^a	D*Hab ^a	Δ ^a
Rate ^b	-2.37 (0.54)	0.003 (0.05)	-0.010 (0.007)	0.696 (0.46)	3.99 (0.95)	0.035 (0.02)	-0.170 (0.06)	0.0*
Efficiency	-0.269 (0.63)	0.069 (0.03)	0.011 (0.007)	0.232 (0.47)	-0.890 (0.49)	-0.035 (0.02)		0.0*
	-0.377 (0.96)	0.078 (0.07)	0.010 (0.007)	0.244 (0.48)	-0.740 (1.1)	-0.035 (0.02)	-0.011 (0.07)	1.98

*Best model. Model selection based on models with ΔAIC_c < 2; Table 8 and models with ΔQAIC_c < 2; Table 10)

^aBSL = sloughs adjacent to burns, dSB = days since burned, D*Hab = interaction of depth and habitat, Δ = difference of AIC value between best model and the given model

^bModels of capture rate are (capture rate + 0.01) = (explanatory variables) because zeroes cannot be log-transformed. See Methods for more details.

Table 3-10. Candidate set of models of great egret capture efficiency using corrected quasi-Akaike's Information Criterion (QAICc) to select generalized linear models constructed with environmental characteristics in foraging locations in Water Conservation Area 3A of the Everglades, USA, 2009 and 2010.

Model	Model Variables ^a	k ^b	QAIC _c	Δ _i	w _i
m5	D, FS, FC, Hab, dSB	7	85.5	0.0	0.304
m5a	D, FS, FC, Hab, dSB, D*Hab	8	87.5	1.98	0.113
m4	D, FS, FC, Hab	6	88.0	2.47	0.088
m20	Yr, FS, FC, Hab, dSB	7	88.0	2.52	0.086
m18	D2, FS, FC, dSB	6	88.4	2.87	0.072
m7	FS, Hab	4	89.0	3.47	0.054
m17	D2, FS, FC, Hab	6	89.2	3.72	0.047
m11	FS, FC, Hab, dSB	6	89.3	3.75	0.047
m18a	D2, FS, FC, dSB, Hab, D2*Hab	8	89.4	3.92	0.043
m9	FS, dSB	4	89.9	4.36	0.034
m10	FS, FC, Hab	5	90.1	4.62	0.030
m6	FS	3	90.3	4.75	0.028
m3	D, FS, FC	5	90.6	5.05	0.024
m16	D2, FS, FC	5	91.3	5.82	0.017
m8	FS, FC	4	92.0	6.50	0.012
m1	D	3	102.4	16.9	<0.001
m15	D2	3	103.3	17.7	<0.001
m19	Yr	3	103.5	17.9	<0.001
m2	D, Hab	4	103.6	18.1	<0.001
m14	dSB	3	104.1	18.6	<0.001
m001	D, Hab, Hab*D	5	105.0	19.5	<0.001
m12	Hab	3	105.3	19.7	<0.001
m00	Yr, Hab, dSB	5	105.3	19.8	<0.001
m13	Hab, dSB	4	105.8	20.3	<0.001

^aD = depth, D2 = depth squared, dSB = days since burned, FC = flock composition, FS = flock size, Hab = habitat bird was foraging in, Yr = year, D*Hab = interaction of depth and habitat, D2*Hab = interaction of depth squared and habitat

^bNumber of parameters included within the model

Table 3-11. Mean (\pm standard deviation) of environmental variables and aquatic organisms in locations sampled with 1-m² throw trap and minnow trap in Water Conservation 3AS of the Everglades, USA, in 2011.

Variable	Burned Sawgrass	Unburned Sawgrass	t	df	p ^a	Number of plots ^b
N	17	13				
Water depth (cm)	11.9 (2.8)	15.7 (3.7)	-3.02	21.7	0.01	
Sawgrass density (stems m ⁻²)	0.06	33.9 (8.7)	27.8 (8.5)		1.95	26.2
Stem density (stems m ⁻²)	40.9 (9.1)	49.0 (11.2)	-2.12	22.7	0.05	
Vegetation height (cm)	52.3 (10.1)	131.9 (16.9)	-15.1	18.5	<0.01	
Vegetation cover (%)	49.0 (14.2)	60.4 (11.8)	-2.39	27.8	0.02	
Periphyton cover (%)	13.1 (13.6)	25.2 (14.7)	-2.79	27.5	0.01	
<i>1-m² Throw Traps</i>						
Fish density (m ⁻²)	3.6 (5.1)	3.1 (3.3)			0.97	
Fish (\leq 20 mm) density (m ⁻²)	2.8 (4.6)	2.6 (2.8)			0.64	
Fish (>20 mm) density (m ⁻²)	0.8 (1.5)	0.5 (0.6)			0.51	
Mean Fish SL (mm)	17.9 (4.6)	16.8 (2.7)			0.95	13,10
Crayfish density (m ⁻²)	1.4 (0.8)	1.9 (1.3)	-1.16	18.2	0.26	
Mean Crayfish length (mm)	31.7 (3.9)	32.8 (2.7)	-0.90	27.0	0.38	17,12
Shrimp density (m ⁻²)	4.3 (11.7)	1.5 (3.3)			0.88	9,6
Amphibian density (m ⁻²)	1.5 (1.4)	0.5 (0.6)			0.01	15,8
Aquatic invert. density (m ⁻²)	4.1 (2.6)	3.5 (3.2)	0.72	22.7	0.48	17,12
<i>Minnow Traps</i>						
Plots sampled	11	12				
Fish abundance	1.8 (3.4)	2.1 (2.4)			0.35	
Mean Fish SL (mm)	19.5 (6.1)	20.5 (8.3)	-0.30	14.7	0.77	9,9
Crayfish abundance	0.09 (0.2)	0.17 (0.3)			0.64	
Mean Crayfish length (mm)	36.0 (9.9)	27.2 (5.9)			NA	2,3
Amphibian abundance	0.18 (0.2)	0.08 (0.2)			0.27	
Mean Amphibian SVL	14.7 (3.8)	21.0 (0.0)			NA	5,2

^ap-values without accompanying values for t and degrees of freedom (df) are from a Kruskal-Wallis rank sum test.

^bNumber of plots in which the given species was captured. Average lengths were calculated using this N.

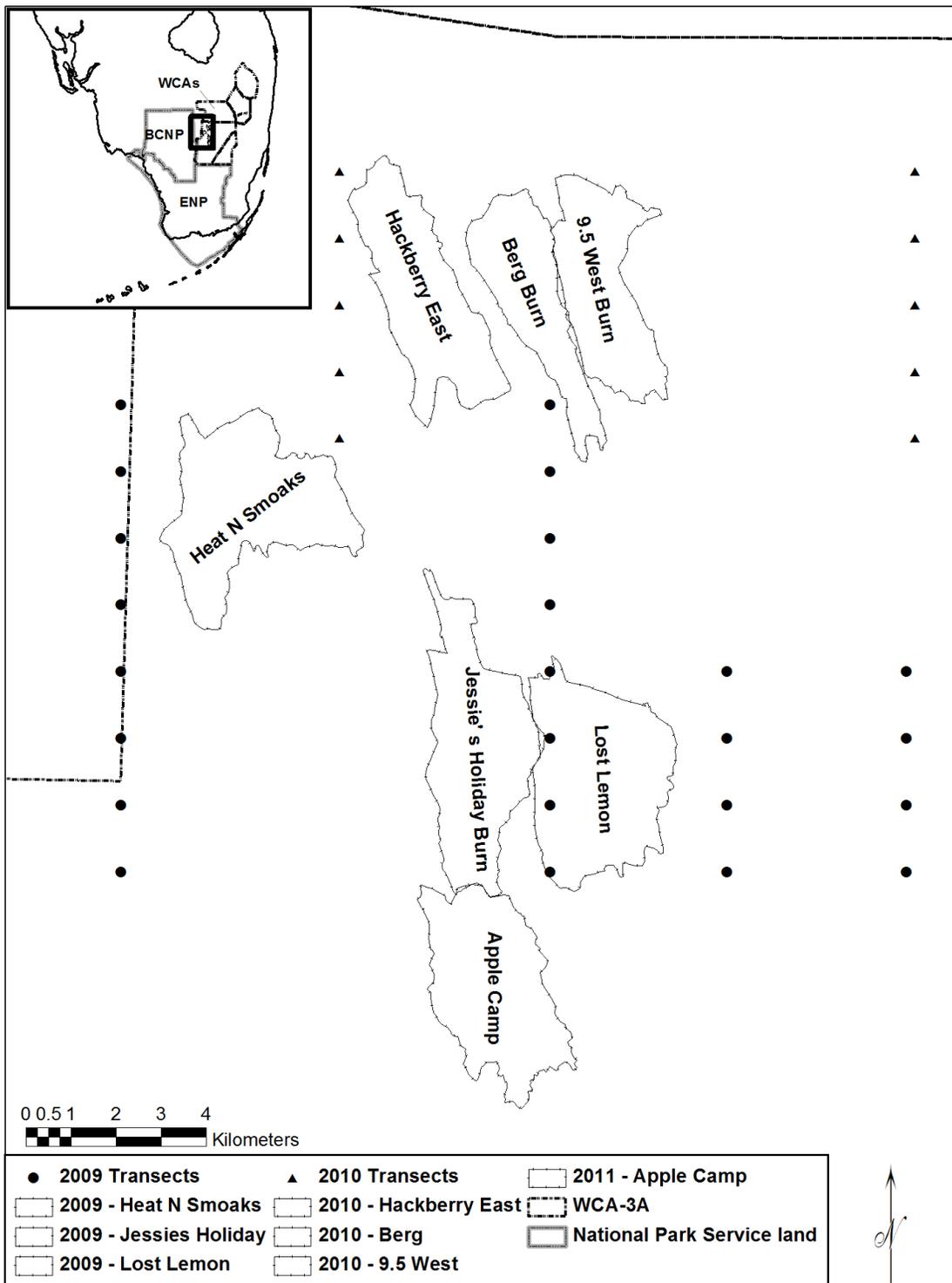


Figure 3-1. Map of study area including prescribed burns conducted in 2009 - 2011 used in various components of this study. See Table 3-1 and Methods for details of the burns and uses.

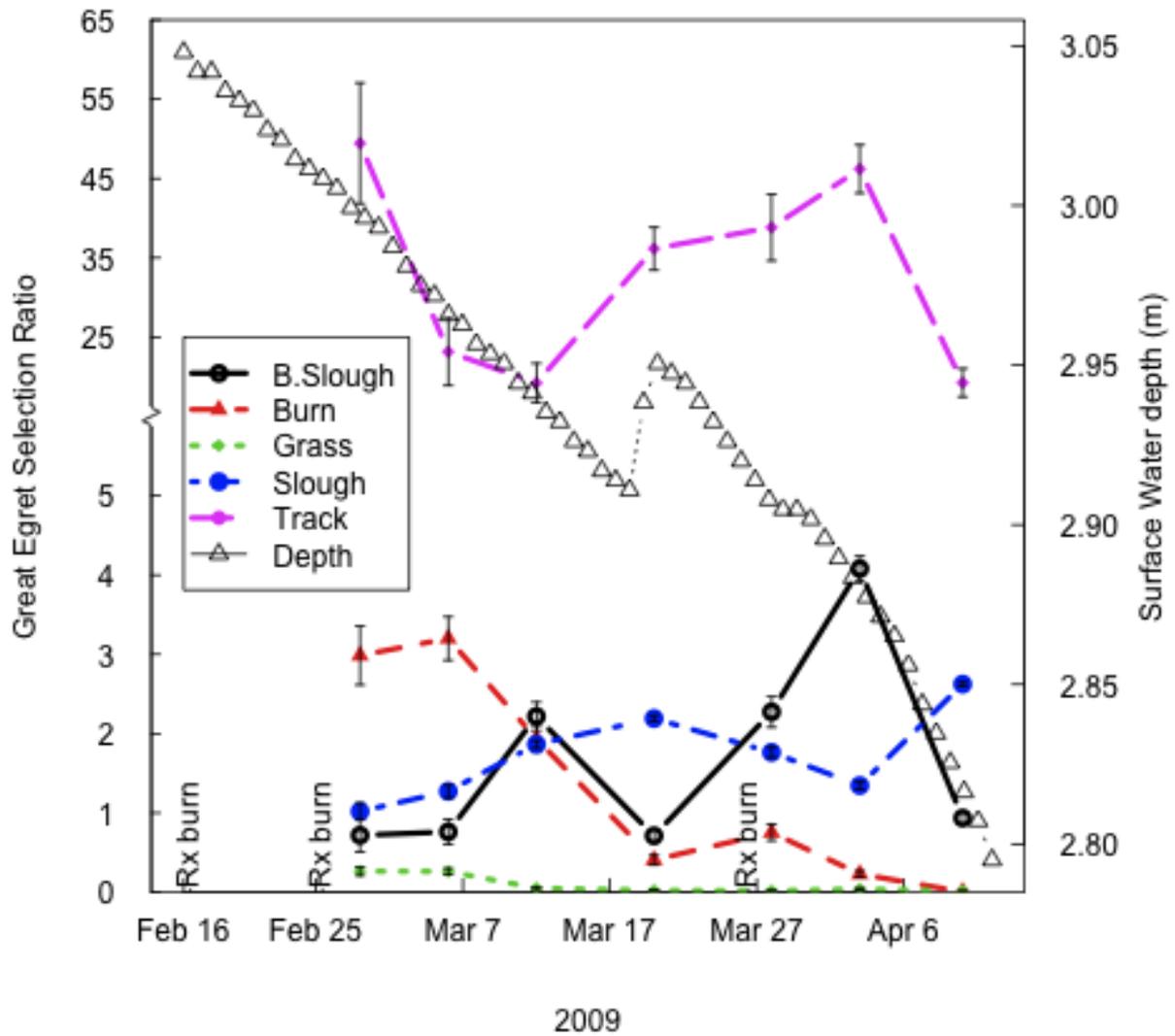


Figure 3-2. Habitat selection ratio (bars represent standard error) for great egrets (*Ardea alba*) in 2009 in the central Everglades, USA. “B.Slough” designates sloughs adjacent to burns. Surface water depth is water level above NGVD29.

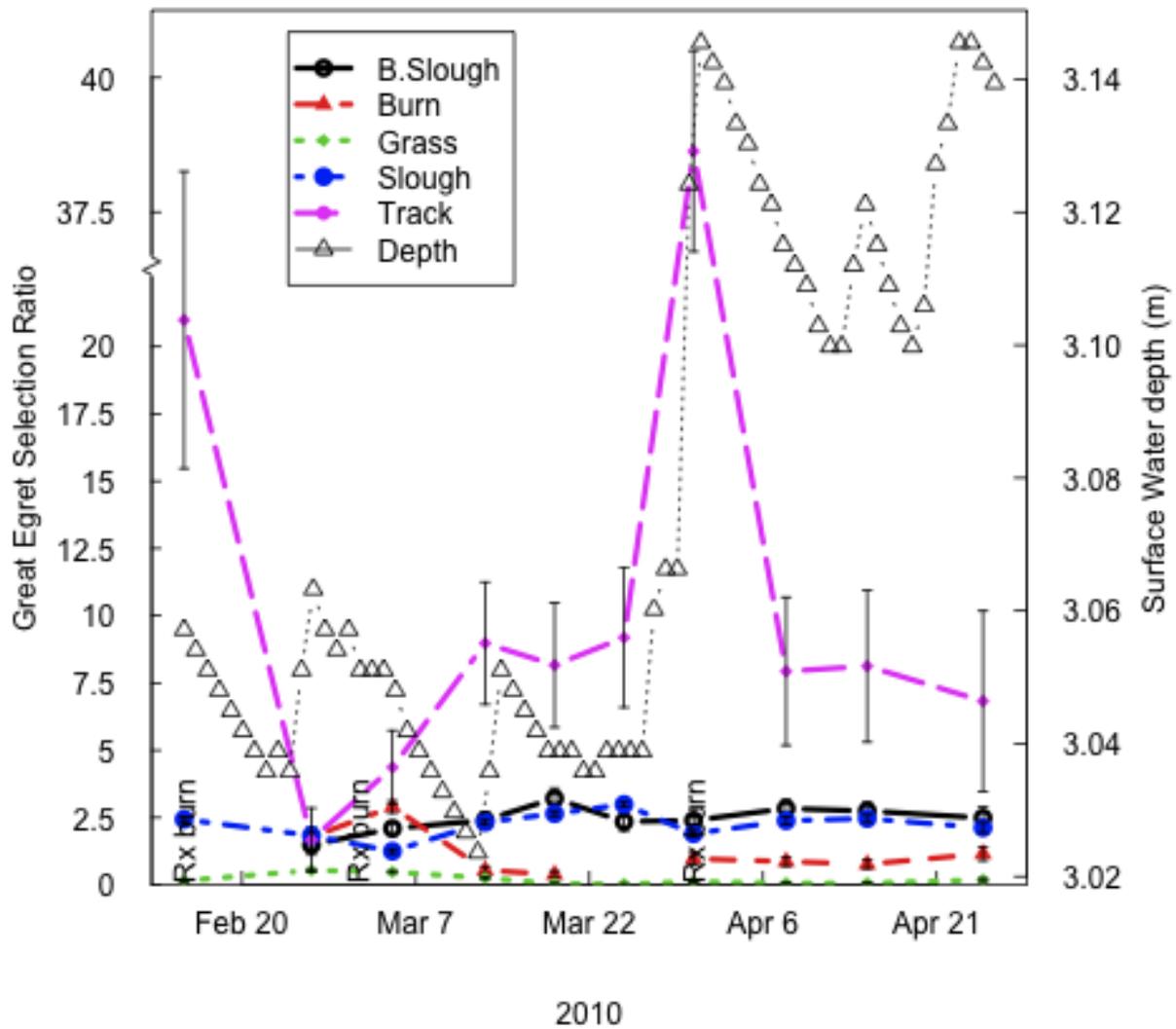


Figure 3-3. Habitat selection ratio (bars represent standard error) for great egrets (*Ardea alba*) in 2010 in the central Everglades, USA. “B.Slough” designates sloughs adjacent to burns. Surface water depth is water level above NGVD29.

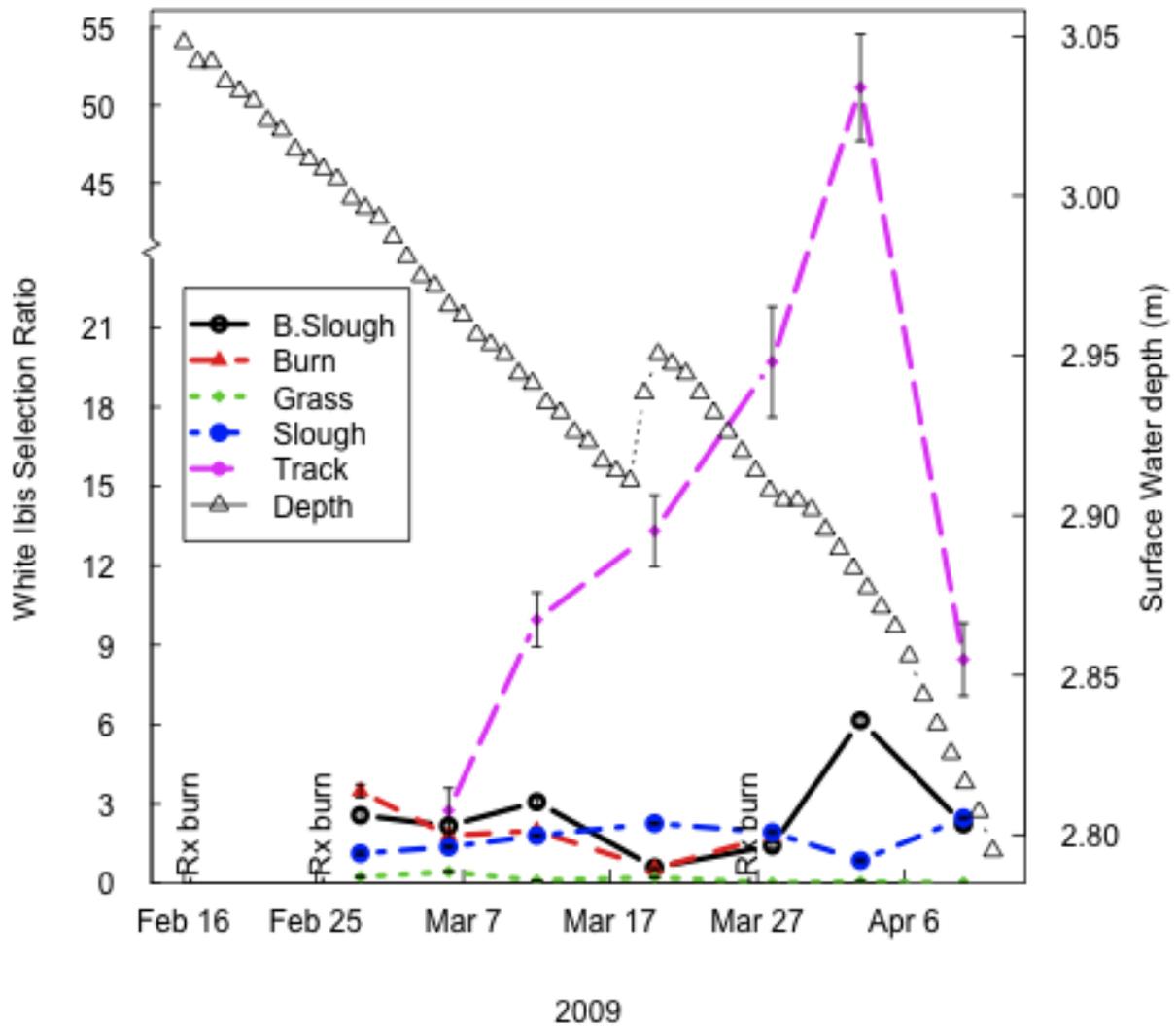


Figure 3-4. Habitat selection ratio (bars represent standard error) for white ibis (*Eudocimus albus*) in 2009 in the central Everglades, USA. “B.Slough” designates sloughs adjacent to burns. Surface water depth is water level above NGVD29.

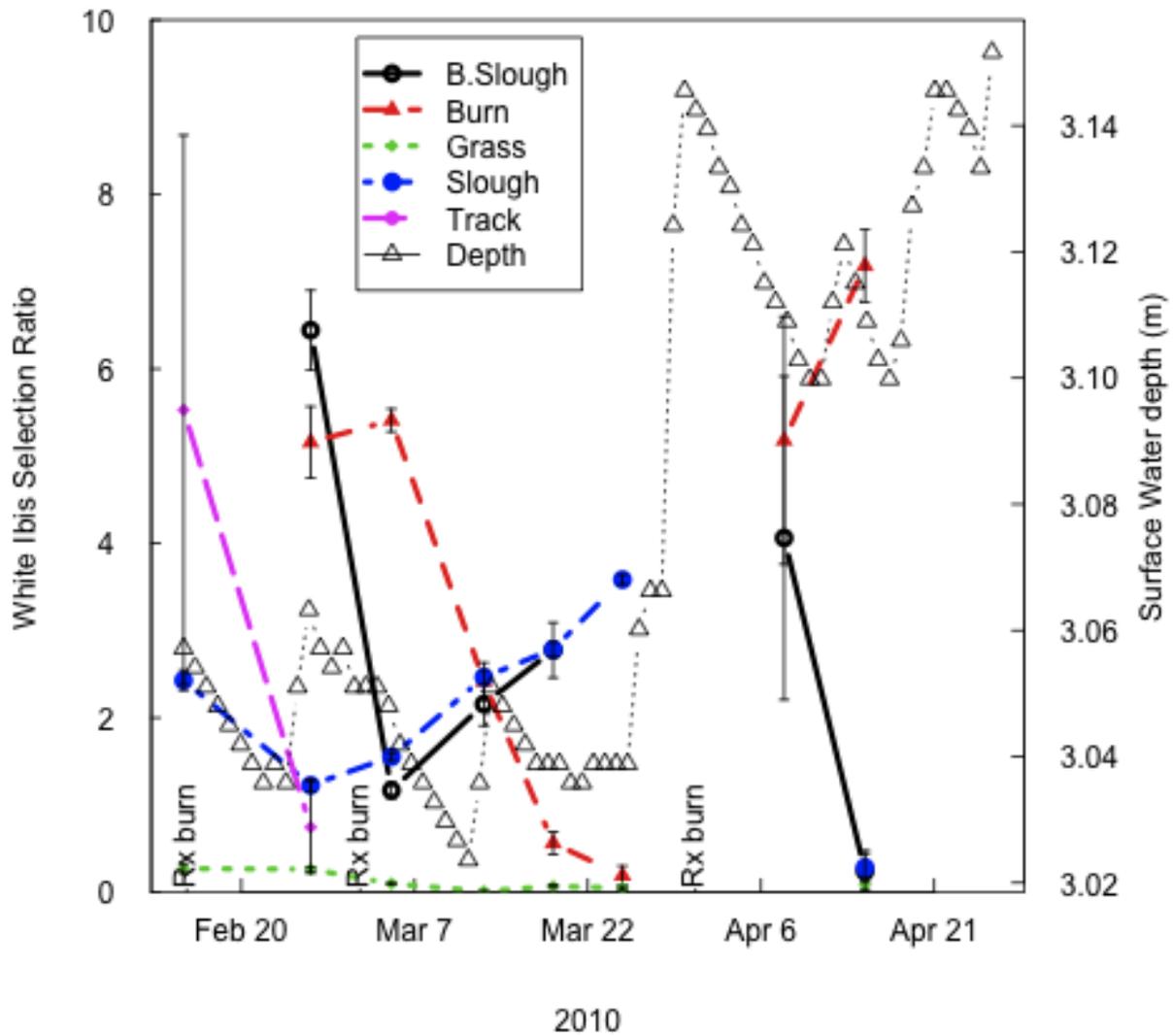


Figure 3-5. Habitat selection ratio (bars represent standard error) for white ibis (*Eudocimus albus*) in 2010 in the central Everglades, USA. “B.Slough” designates sloughs adjacent to burns. Surface water depth is water level above NGVD29.

CHAPTER 4
EFFECTS OF FIRE ON PERIPHYTON PRIMARY PRODUCTION AND FISH
STANDING STOCK IN AN OLIGOTROPHIC WETLAND

Introduction

Fire is a natural disturbance in many upland and wetland ecosystems that, through combustion of vegetation, exposes the underlying substrate to light and redistributes nutrients important to primary production. In uplands, fire typically alters nutrient availability, increases nutritive content in post-fire vegetation, changes vegetative cover and structure, and influences animal utilization of the landscape (Whelan 1995). Similarly, in wetlands where fire occurs, fire has been shown to remobilize nutrients (Smith et al. 2001, Qian et al. 2009), alter plant cover, structure, and composition (Smith and Newman 2001), and promote new vegetative growth (Lugo 1995) with enhanced nutritional content (Smith et al. 1984). Many aquatic invertebrates respond to changes in vegetation post-burn via increasing biomass, density, and abundance (de Szalay and Resh 1997, Munro et al. 2009, Beganyi and Batzer 2011), however, alternate hypotheses such as availability of food resources and alteration of microclimate may better explain use patterns of invertebrates (Hochkirch and Adorf 2007). Most studies concerning the effect of fire on fish generally focus on mountainous watersheds where sediment runoff negatively impacts water quality or reduced shading after a wildfire increases stream temperature (Gresswell 1999), neglecting effects on fish of increased food resources due to fire. While a good understanding of how fire affects nutrient cycling and macrophytes in wetlands has been developed, we do not understand how fire impacts other aspects of wetlands such as periphyton, fish, and higher trophic levels.

Light is a key factor in determining primary production and composition of the algal assemblage (Mosisch et al. 2001). In temporary ponds and streams, an increase in light increased algal biomass (Mosisch et al. 2001, Mokany et al. 2008) while low light levels often result in decreased algal biomass (Hillebrand 2005). High light conditions often result in the presence of larger species of algae, which alters algal species composition and growth form of the algal assemblage. In the Everglades in southern Florida, substantially less periphyton exists in sawgrass stands than in wet prairies and sloughs (McCormick et al. 1998). This is attributed to shading from dense macrophyte communities (Grimshaw et al. 1997, Thomas et al. 2006). However, shading does not change composition of periphyton in the Everglades, but it does reduce gross photosynthesis and percent organic matter at very high levels of shading (98% shade; Thomas et al. 2006).

Nutrients, specifically phosphorus (P), also initiate changes in algal biomass and shifts in species composition (Mosisch et al. 2001, Gaiser et al. 2011). Fire alters nutrient availability, typically resulting in increased bioavailability of P (Smith et al. 2001). In the Everglades where P is limited, remobilization of bioavailable P can be crucial for components of the ecosystem such as periphyton. In a P dosing experiment, periphyton biomass increased within 18 days at doses of 32 mg P/m²/wk (McCormick and Scinto 1999). However, at chronic, low-level P loads, floating periphyton mats are lost and biomass decreases, as the composition of the algal assemblage shifts from cyanobacteria to other algal species (Gaiser et al. 2004). Increases in periphyton P concentrations result in greater productivity of algae that may outcompete certain diatom taxa (Gaiser et al. 2006). This suggests that even small pulses of nutrients from

a fire in an oligotrophic wetland may be able to affect primary production, and possibly have indirect effects on other trophic levels.

An increase in periphyton biomass can provide more food resources to consumers depending on the species composition of the periphyton mat (Rader and Richardson 1992, Geddes and Trexler 2003). Many algal species employ protective mechanisms (e.g., toxins, calcite encrustation) to avoid herbivory, thereby affecting edibility of the periphyton mat (Browder et al. 1994, Chick et al. 2008). Increased algal biomass resulted in a shift in the community of consumers from filter feeders to algal grazers in temporary ponds (Mokany et al. 2008). Similarly, periphyton rich in green algae and diatoms is a preferred food for wetland herbivores (McCormick and Scinto 1999). Tadpoles increased their growth and weight when eating periphyton rich in green periphyton and diatoms rather than blue-green algae (Browder 1981). However, the loss of periphyton mats due to repeated P inputs resulted in decomposition of periphyton-associated vegetation (eastern purple bladderwort) and changes of faunal (fluctuation in fish biomass) assemblages (Gaiser et al. 2005). Additionally, density of the macroinvertebrate community is reduced without periphyton mats (i.e., no habitat available; Liston et al. 2008). Thus, a pulse of nutrients and increase in light, such as result from fires, may increase biomass and alter algal species composition sufficiently to alter the aquatic consumer community, including species that serve as key links to higher trophic levels.

I conducted a field experiment in which I manipulated light and nutrients in order to determine how fire affects oligotrophic wetlands by altering primary production and fish standing stock. I predicted that 1) an increase in light and nutrients would result in more

periphyton biomass and cover and 2) additional available resources, assuming an increase in periphyton biomass, would increase total and individual fish size, condition factor, and relative abundance.

Methods

The Everglades is a large, oligotrophic, P-limited wetland in southern Florida, USA (Noe et al. 2001). Sawgrass (*Cladium jamaicense*) is the dominant vegetation and forms large, slightly elevated “ridges” surrounded by deeper open water sloughs that contain periphyton mats, submerged aquatic vegetation, and some emergent vegetation (Gunderson 1994). Sawgrass is a fast-growing, fire-adapted plant with leaves that grow out from the culm and senesce, with stands typically recovering within 2 years post-burn (Wade et al. 1980). This growth form, coupled with a high frequency of lightning, promotes fire (Wade et al. 1980), resulting in a wetland system that burns frequently, primarily at the onset of the wet season (Gunderson and Snyder 1994, Slocum et al. 2007).

I set up a 2x2 factorial experiment in which I manipulated nutrients and light in 20-10 m x 10 m plots in sawgrass ridges (Fig. 4-1). Nutrient treatments were either burned (added nutrients from a prescribed burn) or mowed with mowed vegetation removed from plots (no nutrients added), based on the assumption that a fire temporarily increases concentrations of available nutrients, and that mowing with removal of above-water vegetation would mimic the light-increase typical following burns, but not add nutrients. Light treatments were plots with and without shade houses to mimic natural shading from sawgrass. Shade cloth was selected using light levels measured for photosynthetically-active radiation (PAR) using an AccuPAR LP-80 (Decagon Devices, Pullman, WA) in sawgrass at five locations in sawgrass stands in the study area (63-

95% shading, $\bar{x} = 84\% \pm 12\%$). Treatments were: burned (nutrients and light added – hereafter named “Nutrients + Light”), burned with shade house (nutrients added, no light – “Nutrients Only”), mowed (no nutrients, light added – “Light Only”), and mowed with shade house (control with no nutrients and no light added – “No Nutrients or Light”). I added a fifth treatment in a stand of unmanipulated sawgrass as an experimental control since the “control” treatment in the 2x2 factorial design was manipulated just like the other treatments. These plots served more as a control of the treatment process than a true control. Hereafter, I refer to this fifth treatment as “Experimental Control”.

Burned plots were located within the sawgrass ridges (>1 ha) of a much larger prescribed burn. This ensured that burn effects were representative of the management tool and minimized edge and small-plot effects of fire. I used ArcMap (Esri, Redlands, CA) to randomly select eight points, four in the prescribed burn unit, and four in an adjacent area that was not burned, from which bearings were randomly selected to place plot locations in the next nearest, sufficiently large (>1 ha) sawgrass ridge. Plots were positioned in sawgrass 30-45 m from the edge of the ridge to reduce edge effects.

The Florida Fish and Wildlife Conservation Commission conducted the prescribed burn on 01 April 2010. The burn unit was approximately 690 ha and incorporated approximately 70% sawgrass, 25% slough, with woody tree islands, cattail (*Typha* spp.), and willow (*Salix* spp.) composing the remainder. Approximately 45% of the overall fuel density was considered heavy. The fire was conducted over standing water ($\bar{x} = 17.5$ cm), and was a complete burn, leaving sawgrass and buttonbush (*Cephalanthus occidentalis*) stubble standing approximately 32 cm above the water surface, typical of burns with standing water in the Everglades. Between 1-4 April 2010,

I set up treatment plots. I mowed an area of 12 m x 12 m with articulating hedge trimmers to a vegetation height above the marsh surface approximately equivalent to burned vegetation ($\bar{x} = 47.5$ cm). I dragged the mowed vegetation >50 m away to areas of deeper water. The extra area was mowed to reduce refuge for aquatic organisms in standing sawgrass on the edge of the plots. On the day following vegetation removal (burned or mowed), I constructed 10 m x 10 m x 2 m (l x w x h) shade houses of 80% spectrally neutral black knitted cloth (International Greenhouse Company, Danville, IL, USA) in plots without light. I also mock-disturbed light treatments that did not get shade houses since the shade house (i.e., no light) plots were trampled by people during set up. Experimental Control plots were not trampled.

I collected water samples for analysis of phosphorus from burned plots in the morning before the burn occurred, in the afternoon shortly after the burn was completed (day 1), and on days 2, 3, 5, 7, 9, 12, and 15. Samples in burned treatments (i.e., “Nutrients”) were collected within 5 m upstream of plots to avoid influence of the shade house treatment set-up on P concentrations. I collected samples in mowed treatments (i.e., “No Nutrients”; within 0-3 days) prior to treatment, immediately after mowing (labeled day 0.5 if a shade house was constructed the following day to complete the treatment), one-day after setting up the treatment, and in two Experimental Control sites the morning before the burn and on day 5. Water samples were placed on ice and processed in the evening of the day sampled. I transferred and acidified 40 mL of water to analyze for total phosphorus (TP) and filtered and acidified 40 mL of water to analyze for soluble reactive phosphorus (SRP). Samples were kept at 4°C and analyzed by the National Environmental Laboratory Accreditation Program (NELAP)-certified University

of Florida Wetland Biogeochemistry Laboratory (Gainesville, FL) within 2.5 months of collection. Additionally, at all water sample locations I collected large clumps of periphyton (<1 L), where present, prior to and immediately after the prescribed burn. These samples were ashed and analyzed for TP at the University of Florida Wetland Biogeochemistry Laboratory.

I sampled plots once every 10 days starting 2 days after all plots were set up for a total of eight sampling periods from early April to the end of June, 2010. In all plots, I measured water depth, average and maximum vegetation height, and I haphazardly placed a 0.25 m² quadrat to estimate percent vegetation cover, percent periphyton cover, and percent periphyton collected. Percent vegetation cover was estimated as percent of area within the water column filled by vegetation, typically using the consensus of two observers. Percent periphyton cover was visually estimated as percent of marsh bottom, vegetative material in water column, and water surface covered by periphyton. The periphyton I collected was stored in plastic bags on ice and transferred to an approximately -20°C freezer within 7 h of collection.

I sampled the fish assemblage using minnow traps. In each plot I set 3 Gee minnow traps (23 x 45 cm, 3.2 mm mesh, Memphis Net & Twine Co., Inc., Memphis, TN) for 2 hours. After 2 hours, I identified and measured total length (TL, ± 1 mm) and mass (± 0.1 g) of each aquatic organism captured. During the last sampling period at the end of June (approximately day 90 of the study), I also used 1-m² throw traps to sample all mowed and burned plots. I threw two traps in each plot, cleared traps following methods of Jordan et al. (1997a), and measured TL of the organisms

captured. I used equations relating TL to standard length (SL) for individual fish species (D. Gawlik, pers. comm.) to convert measurements.

I measured PAR in three locations in each plot once per month between April and June, 2010. Readings were taken between 1000 and 1400 h to standardize the sun azimuth every minute for 15 minutes with some exceptions due to equipment difficulties. I used as many of the readings as possible so plots had 3-15 readings. Readings at all locations in each plot were pooled and averaged to calculate percent shading in the plots.

Periphyton samples were analyzed for chlorophyll *a* following the methods of Sartory and Grobbelaar (1984) at a NELAP-certified University of Florida laboratory (Gainesville, FL). A small (~20 mg, wet weight) subsample of periphyton was weighed and processed while the remaining periphyton from each plot was used to determine wet:dry weight ratios to calculate periphyton biomass. From this, I calculated corrected chlorophyll *a* ($\mu\text{g/g}$) and periphyton mass (g) on a dry weight (dw) basis per area (m^2).

I tested normality of environmental variables (vegetation variables, water depth, and percent shading) with a Shapiro-Wilk normality test. For percent periphyton cover, average and maximum vegetation height and percent vegetation cover, a transformation did not achieve normality, so I rank transformed data and analyzed for differences among treatments using Kruskal-Wallis rank sum tests. I analyzed water depth, percent vegetation cover, and percent shading with an analysis of covariance (ANCOVA) using sampling period as the covariate. For TP and SRP, I compared daily concentrations post-burn to pre-burn concentrations using paired Wilcoxon signed rank tests.

Fish richness and Shannon-Wiener diversity were not normally distributed so data were rank transformed and analyzed for differences among treatments using Kruskal Wallis tests. I analyzed fish metrics (standard length, mass, condition factor, abundance, and relative abundance) for species that were caught in at least 80% of plot-sampling period combinations. I analyzed all species combined and individual species using generalized least squares (*gls*) in R (R Development Core Team 2009). Due to repeated sampling of the same plots, I used models incorporating autoregressive variance-covariance structure and compared models with and without the assumption of heterogeneous variances to determine if there were significant differences among treatments or between sampling periods. I inspected histograms of the residuals and plots of the residuals versus predicted values to determine if transformation was necessary. If there was a significant difference among treatments, I set up three contrasts to compare Experimental Control vs. treatments, light vs. no light, and nutrients vs. no nutrients. To maintain orthogonality of the contrasts, I omitted the Experimental Control treatment from the latter two contrasts.

Relative abundance of fish was organized into a species x site matrix. I fourth-root transformed each response variable to reduce the weight of dominant species on more rare species. I conducted an analysis of similarities (ANOSIM; Clarke 1993) for each of these community matrices, using 999 permutations and Euclidean distances for mass and condition factor and Jaccard's coefficient to calculate distances for relative abundance. Permutations were limited to within each period since there were significant differences among some periods and response variables.

Results

Nutrients

Immediately following completion of plot treatments, TP concentrations in water increased significantly ($F=12.2$, $df=1$, $p<0.001$) with concentrations in the Nutrient treatments (i.e., burned) as high as 0.161 mg/L ($\bar{x} = 0.077$ mg/L; Fig. 4-2). The day after the burn (day 2), the average concentration was 0.024 mg/L (max. = 0.053 mg/L). TP concentrations leveled off at approximately 0.014 mg/L, remaining significantly different than the average pre-burn TP concentration (0.008 mg/L) although the average difference was only 0.006 mg/L. On day 5, there was an elevation to 0.034 mg/L after concentration had declined from the initial peak. On day 15, TP concentrations dropped to 0.005 mg/L, lower than pre-burn concentrations. Concentrations in No Nutrients and Experimental Control treatments were not significantly different than pre-treatment TP concentrations. SRP concentrations in nutrient treatments spiked significantly ($F=6.64$, $df=1$, $p=0.012$) immediately post-treatment to an average of 0.047 mg/L (max. = 0.163 mg/L; Fig. 4-2). SRP concentrations returned to close to detection limits the following day ($\bar{x} = 0.003$ mg/L, max. = 0.013 mg/L) and remained low thereafter with the exception of day 5, corresponding with a spike in TP concentrations, when SRP concentrations were elevated to 0.020 mg/L.

Environmental Factors

Water depth was significantly shallower in the Nutrients Only treatment plots compared to both treatments without nutrients, but did not change much over the course of the experiment (Tables 4-1 & 4-2). Following treatment, shaded treatments (No Nutrients or Light and Nutrients Only), Experimental Control and Light Only, and light treatments (Light Only and Nutrients + Light) were not significantly different in

percent shading, but all other treatments were significantly different (Table 4-2) from each other, indicating that the intended light treatments were effective. Percent vegetation cover did not differ among treatments over the course of the experiment, however average and maximum vegetation heights were significantly higher in Experimental Control than all other treatments (Table 4-1 & 4-3). Vegetation grew over time, driven primarily by all manipulated plots and excluding Experimental Control ($t=9.065$, $df=1,125$, $p<0.001$, adjusted $R^2=0.39$).

Periphyton

Percent periphyton cover was greater in the Nutrient + Light treatment than in all other treatments (Table 4-3). Similarly, on a dry weight (dw) basis, periphyton mass per area and percent periphyton cover were greater in the Nutrient + Light treatment than in all other treatments (Table 4-3). Concentrations of chlorophyll *a* were not significantly different among treatments (Table 4-3).

Overall Fish Metrics

I captured 10 species of fish 2 species of invertebrates, 3 species of amphibians, 1 species of reptile, and 2 species of crustaceans in minnow traps (Table 4-4). Four species of fish (eastern mosquitofish (*Gambusia holbrooki*), least killifish (*Heterandria formosa*), Flagfish (*Jordanella floridae*), sailfin molly (*Poecilia latipinna*)) were captured in nearly all plots during the study. Three of the fish species were captured very infrequently.

The number of fish captured was significantly higher in the Nutrient + Light treatment compared to the No Nutrients or Light treatment, but did not differ from the other treatments (Tables 4-1 & 4-5). Overall fish mass, length, condition factor, relative abundance, and richness were not significantly different among treatments (Tables 4-1,

4-3 & 4-5). Diversity of fishes was significantly higher in treatments with light and lowest in the Experimental Control and Nutrients Only treatments (Tables 4-1 & 4-3).

In the final period when throw traps were also used to sample plots, fish density was greater in plots with light (Tables 4-6 & 4-7). Catch per unit effort of minnow traps and density of fish in throw traps in this final period were related (Adjusted $R^2=0.257$; Fig. 4-3). There were no differences associated with changes in nutrients (Table 4-6). Standard length of all fish and individual species of fish did not differ among treatments with the exception of Everglades pygmy sunfish and marsh killifish (Table 4-7). Everglades pygmy sunfish were significantly longer in treatments with Light (Light Only and Nutrients + Light) than No Light (Nutrients Only and No Nutrients or Light) while marsh killifish were longer in Nutrient treatments (Nutrients Only and Nutrients + Light) than No Nutrients treatments (Light Only and No Nutrients or Light; Tables 4-6 & 4-8). However, there was a significant interaction between light and nutrients for marsh killifish length where lengths under conditions of Light were greater in Nutrient than No Nutrient treatments, but lengths in No Light treatments were similar with and without nutrients.

I used contrasts to compare differences of combined means of factors for four fish species that were captured in 80% or more of the plots across all sampling periods (Table 4-8). Flagfish were smaller (length and mass) and had lower relative abundance in Experimental Control treatments than the combined mean of all other treatments (Tables 4-6 & 4-8, Fig. 4-4). Additionally, flagfish were bigger (length and mass) in No Nutrient treatments compared to Nutrient treatments. I caught more flagfish in Light treatments than no light treatments. Sailfin mollies were heavier in No Nutrient

treatments compared to Nutrient treatments (Tables 4-6 & 4-8, Fig. 4-5). Least killifish were longer in No Light treatments than Light treatments and longer in Nutrient treatments than No Nutrient treatments (Tables 4-6 & 4-8, Fig. 4-6). Least killifish had a higher condition factor in No Nutrient treatments than Nutrient treatments. In Experimental Control plots, least killifish had higher relative abundance than treatment plots, and in plots with Nutrients, relative abundance of least killifish was lower than No Nutrient treatment plots. Eastern mosquitofish showed no differences among treatments (Tables 4-6 & 4-8, Fig. 4-7). Marsh killifish and golden topminnow were captured in 124 and 93, respectively, out of 160 plot-sampling period combinations (Table 4-4), an insufficient number of plots to be analyzed. However, golden topminnows tended to be captured more frequently in the later sampling periods and in nutrient-enriched treatments (data not shown).

Fish Community Response

I used community dissimilarity matrices of relative abundance to determine if treatments had an effect on the fish community sampled. While p-values were significant, the R statistic (indicative of the strength of between vs. within group treatment differences) was close to zero, indicating that relative abundance of fish communities sampled within a treatment were similar to fish communities in other treatments (Table 4-9). The inclusion of crustaceans (i.e., riverine grass shrimp (*Palaemonetes paludosa*) and crayfish (*Procambarus* spp.)) did not change results. Upon closer inspection of effects from nutrients and light, a similar pattern of significant p-values and an R statistic close to zero was revealed for nutrient effects and light effects on fish relative abundance.

Discussion

Contrary to my hypothesis, the fish assemblage showed a limited response to prescribed fire in the Everglades, despite a spike in P concentrations in water and an increase in periphyton cover and biomass in the burn. Post-burn TP and SRP concentrations in water spiked approximately an order of magnitude above pre-burn concentrations for less than 24 hours, indicating that nutrient availability to biota is short-lived after fire in the Everglades. Similarly, P concentrations in nutrient-enriched, cattail-dominated areas of the Everglades spiked relatively quickly and then dropped to pre-burn concentrations (Miao et al. 2010) albeit at slower rates than in the sawgrass dominated marshes sampled in the present study. Absorption by periphyton was likely the primary mechanisms for decreasing concentrations of P following the spike on day 1 post-burn (Noe et al. 2001, Saiers et al. 2003). Periphyton readily uptakes P, in accordance with the loading rate and duration that P is available (Newman et al. 2004). In two periphyton samples I collected at the same site pre- and immediately post-burn, periphyton tissue P concentrations increased by 0.027 and 0.073 mg/kg TP to 0.205 and 0.236 mg/kg, respectively. This elevation in periphyton P concentration reflected P concentration increases in water immediately post-burn at the same sites (0.036 and 0.040 mg/L TP, respectively). Thus, fire is an important process for remobilizing P and making P readily available to biota at the base of the aquatic trophic web.

Phosphorus in water can also diminish by flowing out of the burn, but this is not likely a primary mechanism by which P concentrations in water decreased within the study site. P flow post-burn has been detected at least 100 m downstream of burns (Miao et al. 2010). Most sample locations in this study were in the middle or downstream portions of the burn. Based on water flow rates that range from 0.2-7.9

mm/s in sloughs in central Water Conservation Area 3A of the Everglades (Harvey et al. 2009), the sites I sampled should have had elevated P concentrations equivalent to the day 1 spike on day 2 or later, even under high flow rate conditions. Instead, concentrations dropped rapidly, indicating that biotic uptake reduced P concentrations in water.

Sawgrass stores more TP in belowground parts of the plant that are associated with resource storage than in leaves (Miao and Sklar 1998). Fire-released pulses of P depend on the concentrations of P in the parts of the plant burned. Prescribed burns are typically conducted with standing water covering the belowground portion of sawgrass and only burn the aboveground portion of sawgrass. Thus, prescribed burns remobilize limited concentrations of P and are short-lived due to low concentrations in sawgrass leaves. TP concentrations in water in this study were much lower than TP concentrations released after cattail in the Everglades, which stores more P, was burned (Miao et al. 2010). Conversely, wildfires typically occur when water levels are below the marsh surface and often burn above- and belowground portions of sawgrass, releasing much more P than prescribed burns. In an oligotrophic wetland, any remobilization of nutrients, particularly a limiting nutrient such as P in the Everglades, can result in a boost in primary production.

Increases in periphyton cover and periphyton mass per area (dw) after a fire indicate that the release of P and light post-burn was sufficient to result in a significant response of periphyton. Thomas et al. (2006) saw no difference in periphyton mat composition or daily gross photosynthesis (GPP) under a similar range of light conditions as used in this study. However, past studies of nutrient or light effects on

periphyton in the Everglades have primarily focused on thick mats of periphyton (e.g., Newman et al. 2004, Gaiser et al. 2005, Thomas et al. 2006). In other aquatic systems, light typically results in increased algal biomass (Mosisch et al. 2001, Mokany et al. 2008). Periphyton in a recently burned area with no established periphyton mat, such as plots in this study, may react differently to changes in light conditions than an established periphyton assemblage in a thick mat.

Periphyton collected in sawgrass ridges in this study generally grew as a thin epipellic layer, which may be more available to herbivores than when growing within a thick, complex mat structure (Geddes and Trexler 2003, Chick et al. 2008). Periphyton mats in very oligotrophic areas of the Everglades ($\leq 7 \mu\text{g/L}$ TP in water) tend to be composed primarily (49-83%) of cyanobacteria (McCormick and O'Dell 1996). Edible, preferred species such as diatoms grow in pockets created during cyanobacterial growth (Geddes and Trexler 2003). Nutrient enrichment can alter species composition or structure of the mat and thereby increase edibility of periphyton (Geddes and Trexler 2003, Chick et al. 2008). While I do not have species composition data to confirm edibility, the increase of periphyton in burned sawgrass stands may have provided an additional food resource for herbivorous species where periphyton was previously limited or non-existent.

Total fish assemblage did not respond to prescribed fire in the Everglades despite an increase in periphyton cover and biomass in burns. Over the duration of this experiment, fish showed a lot of variability in all metrics and no consistent trend, indicating that burns increased overall fish size or condition factor. While it is possible that the duration of the experiment was insufficient to capture all effects of fire on the

fish assemblage using a prescribed burn, we saw no indication of a lag in response. Total fish abundance increased temporarily (about three weeks) after a burn, but this did not translate into increases in overall fish size or condition factor. Fish are highly mobile organisms that can respond relatively quickly to changes in the environment (DeAngelis et al. 2010, Obaza et al. 2011). Thus, fish may have concentrated in the burn for the first three weeks and then left rather than staying in this habitat for three months or more. Additionally, species respond to environmental changes differently based on availability of preferred food resources (e.g., Reimer 1970) and predation risk (e.g., Dorn et al. 2006). Metrics characterizing the total fish assemblage are a composite of species with these different life history traits. The contrasting behaviors of species likely diluted responses of individual species, resulting in no overall trend. Thus, aggregating the entire assemblage may have obscured responses by individual species to burned areas. Responses by individual species to burns may be more informative.

As expected, individual species of fish responded differently to treatments. Least killifish, the smallest fish species captured, were 1-2 mm longer (6-11% length increase) in burned than unburned areas, a biologically significant size difference for this species. Larger female least killifish produce more broods and more juveniles per brood than smaller females (Leips and Travis 1999). Thus, the increase of nutrients in burns could increase reproductive output of this species via increasing female size. Conversely, smaller flagfish and sailfin mollies were captured in burns. Differences in size for these species, and also for least killifish, may not be due to growth (Travis et al. 1989), but rather related to habitat choice by different size classes.

Differences in the abundance of species such as Everglades pygmy sunfish captured by minnow and throw traps in treatment plots illustrate that interpretation of treatment effects can be biased by the capture method used. I used minnow traps to minimize sampling disturbance of the plots (i.e., increased nutrient concentrations from re-suspended sediment; Rozas and Minello 1997), and to avoid obfuscating effects that may have occurred as a result of treatment. Passive sampling devices such as minnow traps are biased because they do not sample a standardized area, are selective in terms of species captured, and do not have high capture efficiency (e.g., Blaustein 1989, He and Lodge 1990, Layman and Smith 2001, Obaza et al. 2011). For some species though, minnow traps can provide an accurate index of abundance (He and Lodge 1990). However, I expect that repeated use of throw traps, in which I pulled all sawgrass (and thus underwater structure) to clear traps, would have changed the habitat and treatment effects in the plots almost immediately, resulting in samples not representative of the treatments in which samples were taken. Loftus and Eklund (1994) illustrated differences in the fish community between the surrounding marsh and sampling locations due to long-term use of a drop trap in the same locations, thereby lowering marsh elevations and changing fish response. While minnow traps are not ideal for measuring fish response to changes in the environment, they were the best available method given the study objectives and constraints and provided similar responses to throw traps. Despite the limitation of minnow traps, the results of this study provide an initial understanding of how fish respond to changes related to fire burning wetlands.

In conclusion, the fish assemblage showed a limited response to prescribed fire in the Everglades, contrary to my hypothesis, despite a spike in P concentrations in water in the burn and an increase in periphyton cover and biomass in burns. Concentrations of nutrients available for biotic uptake were limited by concentrations in aboveground plant parts and may result in limited trophic level effects such as we saw in this study. Concentrations of P in peat are much higher than in sawgrass (Noe et al. 2001), representing a significant source of P in the Everglades. Wildfires typically occur when water levels are below the marsh surface and frequently burn the entire sawgrass plant and the peat (Wade et al. 1980). Due to higher concentrations of P stored in sawgrass and peat below the marsh surface, I would expect a stronger response by periphyton and fish to higher P concentrations available after wildfires that burn peat, however this has not been quantified and should be studied. Similarly, effects of fires in other oligotrophic wetlands are likely influenced by concentrations of the limiting nutrient released during fires.

Table 4-1. Mean (\pm standard deviation) of environmental variables measured in plots.

Variable	Experimental Control	No Nutrients or Light	Light Only	Nutrients Only	Nutrients + Light
Water Depth (cm)*	17.1 (3.6) ^{bc}	17.3 (3.1) ^c	19.3 (3.8) ^c	15.2 (3.1) ^{ab}	17.4 (3.9) ^{bc}
Shading (%)*	63 (27) ^b	89 (4) ^a	36 (26) ^c	87 (6) ^a	50 (18) ^{bc}
Median Vegetation Height (cm)*	165 ^a	71 ^c	83 ^b	69.5 ^c	89 ^b
Vegetation Height range (cm)	142-215	37-103	27-122	39-98	32-120
Median Max. Vegetation Height (cm)*	200 ^a	101 ^{cd}	114 ^b	94.5 ^d	104 ^{bc}
Max. Vegetation Height range (cm)	161-350	51-150	56-177	56-175	43-157
Vegetation Cover (%)	40.7 (28)	27.8 (19)	29.0 (22)	26.3 (9.4)	25.3 (18)
Periphyton Cover (%)*	21.4 (24) ^b	8.1 (14) ^c	13.5 (14) ^b	11.3 (14) ^c	26.6 (23) ^a
Periphyton Mass per Area (g dw/m ²)*	41.5 (65) ^b	2.8 (5.4) ^c	12.5 (26) ^b	8.6 (14) ^b	50.5 (83) ^a
Average Chlorophyll a (μ g/g dw)	558 (630)	771 (543)	687 (387)	1084 (920)	689 (366)
Chlorophyll a (μ g/g dw)	0-2134	0-2486	0-1474	0-3590	0-1400
Average Fish Standard Length (mm)	25.4 (4.4)	25.5 (2.5)	25.8 (2.6)	26.5 (2.8)	26.2 (2.8)
Average Fish Mass (g)	0.54 (0.36)	0.52 (0.22)	0.56 (0.23)	0.59 (0.26)	0.56 (0.24)
Average Fish Condition Factor	2.18 (0.20)	2.24 (0.21)	2.32 (0.27)	2.22 (0.19)	2.25 (0.22)
Average Fish Abundance	48.7 ^{ab}	37.3 ^b	55.4 ^{ab}	50.2 ^{ab}	63.8 ^a
Average Relative Abundance	20.4	20.6	17.4	18.6	18.0
Richness	4.9 (1.5)	4.8 (1.2)	5.7 (1.2)	5.4 (1.2)	5.5 (1.2)
Shannon Diversity*	1.09 ^{bc}	1.03 ^c	1.27 ^a	1.03 ^c	1.17 ^{ab}

* Significant difference among treatments, differences denoted by letters. Summary of statistical results provided on Table 4-2 and Table 4-3.

Table 4-2. Summary of ANCOVAs testing differences due to treatment and period.

Variable	Treatment			Period			Interaction			Residuals
	df	F	p	df	F	p	df	F	p	
Water Depth (cm)	4	5.48	<0.001	1	1.24	0.267	4	1.59	0.180	148
Shading (%)	4	12.0	<0.001	1	2.46	0.128	4	0.257	0.903	29

Table 4-3. Summary of responses of biotic variables to treatments (Kruskal-Wallis rank sum test)

Variable	Treatment		
	df	χ^2	p
<i>Periphyton</i>			
Periphyton Cover (%)	4	16.7	0.002*
Periphyton Mass per Area (g dw/m ²)	4	18.7	0.001*
Chlorophyll a (corrected) (µg/g dw)	4	7.04	0.134
<i>Vegetation</i>			
Vegetation Cover (%)	4	6.12	0.190
Vegetation Height (cm)	4	83.6	<0.001*
Max. Vegetation Height (cm)	4	76.5	<0.001*
<i>Fish</i>			
Richness	4	9.30	0.054
Diversity	4	11.6	0.021*
Relative Abundance	4	5.95	0.203

Table 4-4. Frequency of capture of aquatic organisms in minnow traps by treatment plot and species in the Everglades, 2010.

Species	Experimental Control ^a	No Nutrients or Light	Light Only	Nutrients Only	Nutrients + Light
Fish					
<i>Elassoma evergladei</i> (Everglades pygmy sunfish)	0	0	0	1	0
<i>Esox americanus</i> (redfin pickerel)	0	0	2	0	0
<i>Fundulus chrysotus</i> (golden topminnow)	18	11	16	25	24
<i>F. confluentus</i> (marsh killifish)	21	23	27	34	25
<i>Gambusia holbrooki</i> (eastern mosquitofish)	32	32	32	31	32
<i>Heterandria formosa</i> (least killifish)	28	29	31	19	23
<i>Jordanella floridae</i> (flagfish)	23	28	31	31	31
<i>Lepomis punctatus</i> (spotted sunfish)	2	2	1	3	3
<i>Lucania goodei</i> (bluefin killifish)	8	4	16	9	16
<i>Poecilia latipinna</i> (sailfin molly)	25	26	28	25	24
Crustaceans					
<i>Palaemonetes paludosa</i> (riverine grass shrimp)	18	19	23	14	21
<i>Procambarus</i> spp. (crayfish)	10	18	13	9	5
Herpetofauna					
<i>Nerodia fasciata</i> (Florida water snake)	2	1	0	1	1
<i>Notophthalmus viridescens piaropicola</i> (peninsula newt)	0	0	1	0	0
<i>Siren lacertina</i> (greater siren)	1	1	0	0	1
<i>Rana grylio</i> (pig frog)	3	3	3	0	3
Macroinvertebrates					
<i>Belastomatid</i> (giant water bug)	1	0	0	2	1
<i>Dytiscidae</i> (predaceous diving beetle)	6	3	1	5	9

^aNumber of plot and period combinations in which each species was captured at least once. Total possible plot and period combinations per treatment is 32.

Table 4-5. Summary of generalized least squares regression examining response of fish measures to treatment and sampling period.

Variable ^b	Model ^c	Treatment		Period		Interaction		Treatment Contrast ^a
		F	p	F	p	F	p	
<i>All Fish</i>								
Standard Length ^d	arh1	1.21	0.310	2.02	0.058	0.910	0.600	--
Mass ^e (log)	arh1	0.634	0.640	1.45	0.193	0.789	0.762	--
Condition Factor	arh1	0.420	0.794	4.76	<0.001*	1.73	0.023	--
Abundance (4 th rt)	arh1	1.91	0.113	2.49	0.020*	0.923	0.581	--
<i>G. holbrooki</i>								
Standard Length	arh1	1.36	0.254	2.44	0.023*	1.10	0.348	--
Mass (sqrt)	ar1	1.31	0.271	1.16	0.333	1.00	0.473	--
Condition Factor	arh1	1.03	0.394	8.58	<0.001*	1.05	0.410	--
Abundance (sqrt)	arh1	1.17	0.328	3.37	0.003*	0.865	0.661	--
Relative Abundance	ar1	0.978	0.423	2.52	0.019*	0.818	0.725	--
<i>J. floridae</i>								
Standard Length	arh1	4.69	0.002*	2.69	0.014*	0.737	0.822	control, nutrients
Mass	arh1	6.41	<0.001*	2.22	0.039*	0.850	0.681	control, nutrients
Condition Factor	arh1	1.18	0.323	2.45	0.028*	0.734	0.825	--
Abundance	arh1	4.17	0.003*	0.864	0.537	1.47	0.079	light
Relative Abundance (sqrt)	arh1	4.74	0.001*	1.52	0.167	1.23	0.223	control
<i>P. latipinna</i>								
Standard Length	ar1	2.35	0.061	3.06	0.006*	0.819	0.720	--
Mass	ar1	3.43	0.012*	1.95	0.071	1.01	0.469	nutrients
Condition Factor	arh1	0.729	0.574	1.79	0.100	1.69	0.034*	--
Abundance	arh1	1.98	0.102	3.11	0.005*	0.799	0.749	--
Relative Abundance	ar1	2.31	0.062	4.32	<0.001*	1.26	0.196	--

Table 4-5. Continued

Variable ^b	Model ^c	<u>Treatment</u>		<u>Period</u>		<u>Interaction</u>		<u>Treatment Contrast^a</u>
		F	p	F	p	F	p	
<i>H. formosa</i>								
Standard Length	arh1	6.83	<0.001*	1.91	0.077	1.78	0.022*	nutrients, light
Mass	ar1	1.67	0.165	1.96	0.069	1.81	0.019*	--
Condition Factor	arh1	2.90	0.026*	2.44	0.024*	1.45	0.096	nutrients
Abundance	arh1	2.32	0.061	4.13	<0.001*	1.10	0.347	--
Relative Abundance (sqrt)	arh1	4.50	0.002*	3.53	0.002*	1.30	0.168	control, nutrients

^aTreatment contrasts refer to differences seen among treatments. control = Experimental Control vs. other treatments, nutrients = nutrients vs. no nutrients, light = light vs. no light

^bTransformation of dependent variable given in parentheses. If there is nothing in parentheses, variable was not transformed. sqrt = square root, 4th rt = fourth root, log = log

^carh1 = autoregressive with heterogeneous variances, ar1 = autoregressive; degrees of freedom are treatment = 4, period = 7, and interaction = 28

^dStandard length is in millimeters

^eMass is in grams

Table 4-6. Mean (\pm standard deviation) of fish captured in 1-m² throw traps.

Variable	No Nutrients or Light	Light Only	Nutrients Only	Nutrients + Light
Density*	17.1 (4.8)	36.0 (17.1)	23.4 (9.6)	29.3 (9.2)
Standard Length (mm)				
All fish	16.2 (7.5)	15.9 (6.7)	17.9 (10.0)	14.3 (4.0)
<i>E. evergladei</i> *	14.0 (1.0)	16.5 (2.0)	11.1 (1.2)	14.7 (4.3)
<i>F. chrysotus</i>	21.5 (15.6)	10.5	43.2	12.8 (2.2)
<i>F. confluentus</i> *	14.7 (2.5)	10.7 (4.4)	15.5 (2.3)	21.5 (3.0)
<i>G. holbrooki</i>	13.7 (2.7)	11.9 (3.4)	12.5 (3.1)	13.4 (2.8)
<i>H. formosa</i>	11.0 (0.8)	11.4 (0.9)	11.8 (1.4)	11.8 (0.9)
<i>J. floridae</i>	20.9 (8.2)	28.3 (5.7)	22.7 (8.6)	16.2 (5.5)
<i>L. goodei</i>	--	14.8 (6.2)	16.2 (1.5)	14.1 (3.8)
<i>L. punctatus</i>	--	27.0	47.8 (9.2)	--
<i>P. latipinna</i>	22.3 (9.3)	20.2 (6.5)	19.1 (3.0)	12.8 (1.4)

* Significant difference among treatments. Statistical summary provided on Table 4-7.

Table 4-7. Summary of Analysis of Variances (ANOVA) examining response of all and individual fish species captured in throw traps to light (Light vs. No Light) and nutrient treatments (Nutrients vs. No Nutrients).

Variable	Light		Nutrients		Interaction		df ^a
	F	p	F	p	F	p	
Density	4.98	0.046*	0.002	0.965	1.37	0.264	1,1,1,12
Standard Length (mm) ^b							
<i>E. evergladei</i>	6.33	0.024*	4.64	0.048*	0.170	0.686	1,1,1,15
<i>F. confluentus</i>	0.152	0.706	14.6	0.004*	5.42	0.045*	1,1,1,9
<i>G. holbrooki</i>	0.189	0.667	0.106	0.747	2.17	0.152	1,1,1,27
<i>H. formosa</i>	0.249	0.622	3.24	0.083	0.203	0.656	1,1,1,28
<i>J. floridae</i>	0.309	0.585	2.99	0.100	4.99	0.038*	1,1,1,19
<i>L. goodei</i>	0.733	0.417	0.008	0.933		NA	1,1,1,8
<i>P. latipinna</i> (log) ^c	3.37	0.081	3.78	0.065	1.68	0.209	1,1,1,21

^aDegrees of freedom for light, nutrients, interaction, and residuals, respectively.

^b"All fish" and *F. chrysotus* were not normally distributed and were analyzed for differences between light and between nutrient treatments using a Kruskal-Wallis rank sum test. P-values were > 0.18 and are not included on this table.

^c*P. latipinna* standard lengths were log-transformed to meet assumptions of normality.

Table 4-8. Characteristics of fish species caught in at least 80% of plots sampled; mean (\pm standard deviation).

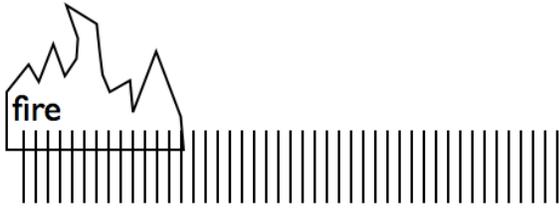
Variable	Experimental Control	No Nutrients or Light	Light Only	Nutrients Only	Nutrients + Light
<i>G. holbrooki</i>					
Standard Length (mm)	22.6 (1.6)	23.4 (1.3)	23.3 (2.2)	23.5 (1.1)	23.2 (1.4)
Mass (g)	0.26 (0.06)	0.28 (0.05)	0.28 (0.05)	0.29 (0.05)	0.28 (0.06)
Condition Factor	1.97 (0.26)	1.98 (0.16)	2.12 (0.73)	1.98 (0.18)	1.98 (0.28)
Abundance	28.9 (27.4)	23.0 (11.1)	30.6 (22.8)	34.5 (27.1)	36.5 (23.4)
Relative Abundance	56.9 (18.7)	63.0 (17.5)	52.6 (15.3)	62.9 (20.2)	56.5 (15.2)
<i>J. floridae</i>					
Standard Length*	25.7 (2.4)	27.9 (2.3)	29.0 (2.8)	26.2 (3.6)	26.9 (2.3)
Mass*	0.61 (0.19)	0.77 (0.19)	0.90 (0.27)	0.63 (0.23)	0.67 (0.18)
Condition Factor	3.4 (0.36)	3.4 (0.44)	3.4 (0.48)	3.3 (0.32)	3.3 (0.33)
Abundance*	5.1 (7.8)	4.2 (4.0)	7.3 (6.7)	5.2 (4.9)	11.7 (12.8)
Relative Abundance*	7.2 (6.8)	10.0 (8.0)	13.2 (7.2)	11.5 (11.3)	16.4 (11.8)
<i>P. latipinna</i>					
Standard Length	24.5 (3.8)	25.9 (6.3)	27.8 (3.8)	24.3 (4.0)	24.7 (3.7)
Mass*	0.43 (0.16)	0.55 (0.33)	0.62 (0.23)	0.44 (0.18)	0.41 (0.18)
Condition Factor	2.51 (0.37)	2.55 (0.58)	2.51 (0.33)	2.65 (0.43)	2.47 (0.40)
Abundance	5.7 (5.6)	3.8 (4.5)	6.6 (6.1)	4.3 (4.2)	3.4 (4.9)
Relative Abundance	11.8 (11.9)	9.4 (9.1)	11.8 (9.4)	9.7 (10.5)	5.4 (7.3)
<i>H. formosa</i>					
Standard Length*	17.4 (1.5)	17.9 (1.4)	17.2 (1.8)	19.0 (1.8)	18.5 (1.9)
Mass	0.13 (0.04)	0.15 (0.05)	0.13 (0.05)	0.16 (0.06)	0.15 (0.05)
Condition Factor*	2.42 (0.54)	2.53 (0.48)	2.51 (0.78)	2.30 (0.38)	2.20 (0.45)
Abundance*	3.7 (3.0)	3.0 (3.0)	4.8 (6.2)	1.8 (2.4)	3.4 (4.2)
Relative Abundance*	11.2 (9.3)	8.8 (8.1)	9.5 (9.1)	3.5 (4.2)	5.5 (6.7)

* Letters indicate significant difference of means between treatments grouped by factor (e.g., light vs. no light).

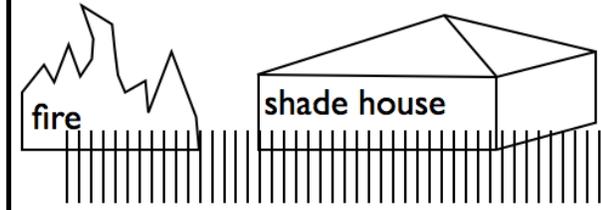
Table 4-9. Summary of ANOSIM (Analysis of Similarities) results testing differences of relative abundance. The R statistic ranges from -1 to 1 with 0 indicating random grouping of replicates in groups and 1 indicating replicates within a site are similar compared to replicates from other sites. A p value <0.05 is used to indicate significance(*).

Comparison	<u>Fish Only</u>		<u>Fish and Crustaceans</u>	
	R statistic	p value	R statistic	p value
All Treatments	0.063	0.001*	0.064	0.001*
Exp. Ctrl vs. Treatment	0.108	0.026*	0.109	0.030*
Period	0.055	0.001*	0.055	0.001*
Nutrients	0.072	0.001*	0.072	0.003*
Light	0.010	0.261	0.011	0.274

Nutrients + Light



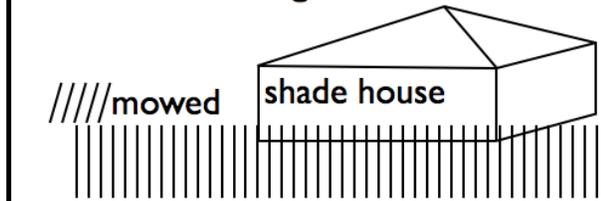
Nutrients Only



Light Only



No Nutrients or Light



Experimental Control = not manipulated

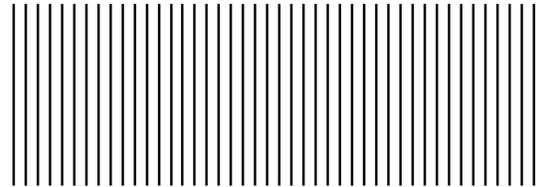


Figure 4-1. Experimental design showing burned (Nutrient) treatments (top row) vs. unburned (No Nutrient) treatments (second row) and Light treatments (first column) vs. No Light treatments (second column). Experimental Control treatment is the unmanipulated version of the No Nutrients or Light treatment.

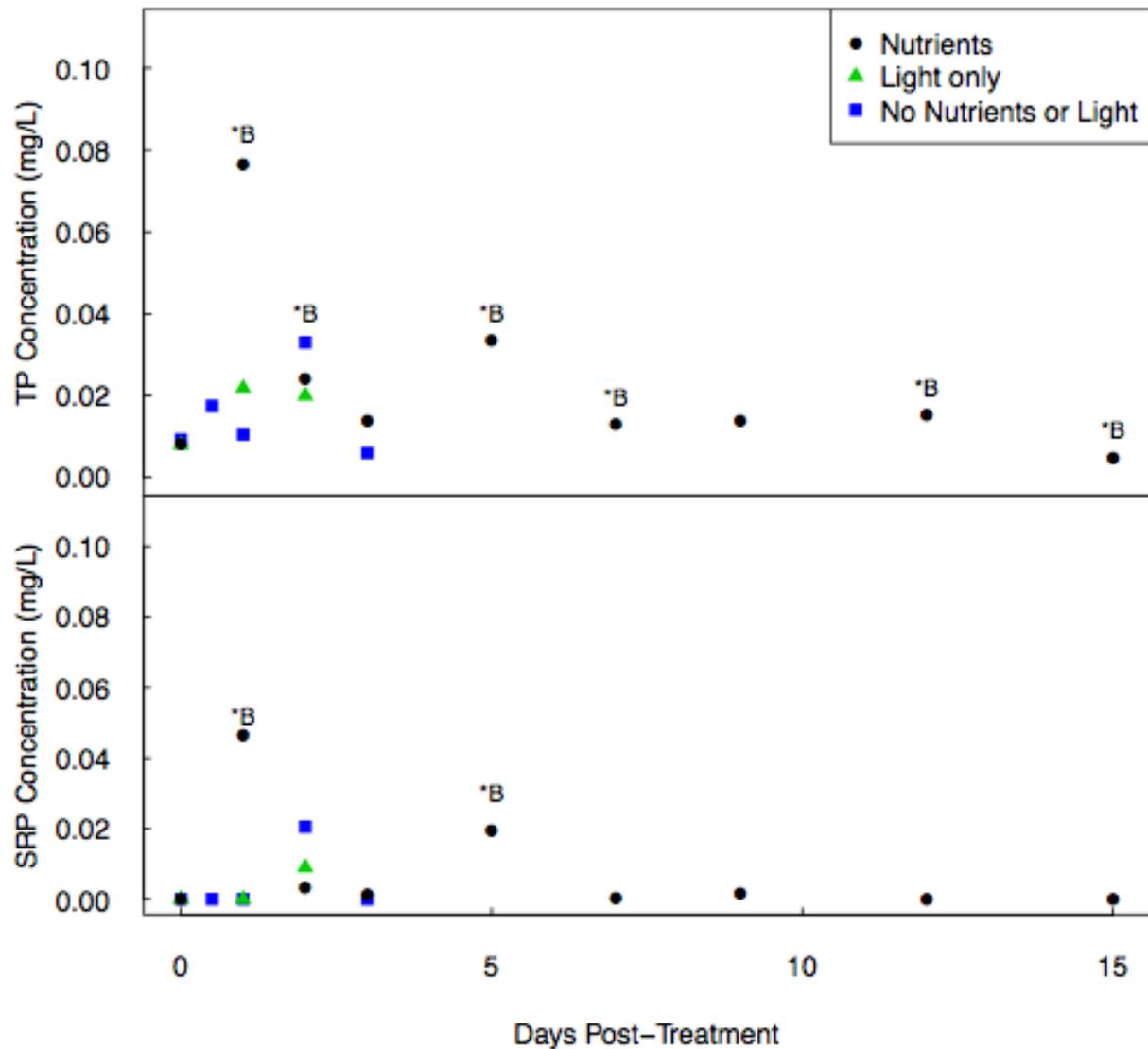


Figure 4-2. Concentrations of total phosphorus (TP) and soluble reactive phosphorus (SRP) in water sampled collected pre-burn (day 0) and post-burn (days 0.5-15) in burned plots (Nutrients), mowed with vegetation removed (Light Only), and mowed with vegetation removed and a shade house constructed (No NL = No Nutrients or Light) in northern Water Conservation Area 3A South of the Everglades, Florida, USA. *B = concentration in burn on that day is significantly different than pre-burn phosphorus concentration

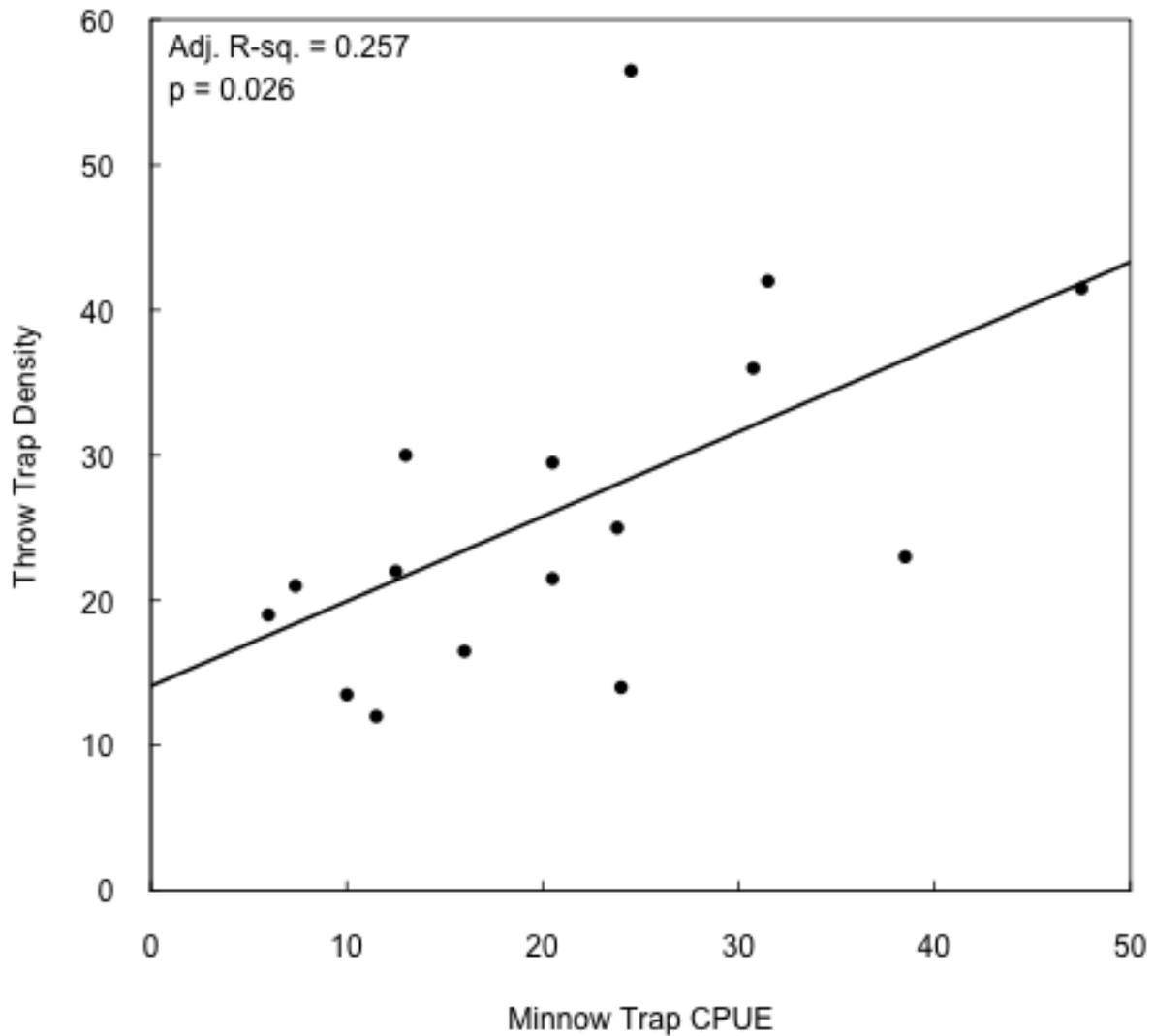


Figure 4-3. Linear relationship of minnow trap catch per unit effort (CPUE) and throw trap density sampled during the final sampling period (period 8) in treatment plots (n=16). Experimental control plots were not sampled with throw traps. Adjusted R^2 value provided on the figure.

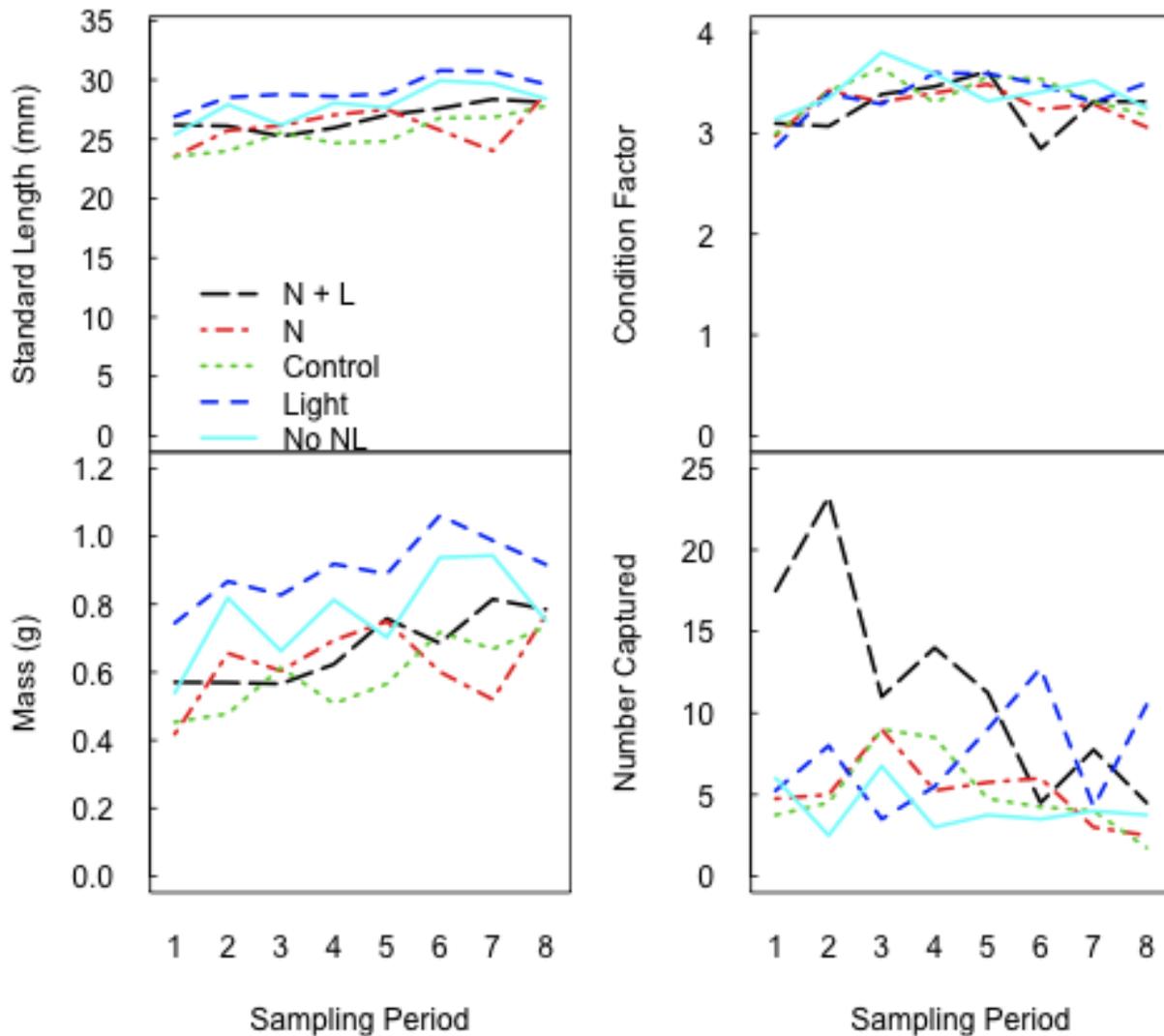


Figure 4-4. Standard length (mm), mass (g), condition factor, and abundance of Flagfish (*Jordanella floridae*) captured in minnow traps in plots post-burn in northern Water Conservation Area 3A South of the Everglades, Florida, USA. N+L = Nutrients + Light, N = Nutrients Only, Control = Experimental Control, Light = Light Only, No NL = No Nutrients or Light

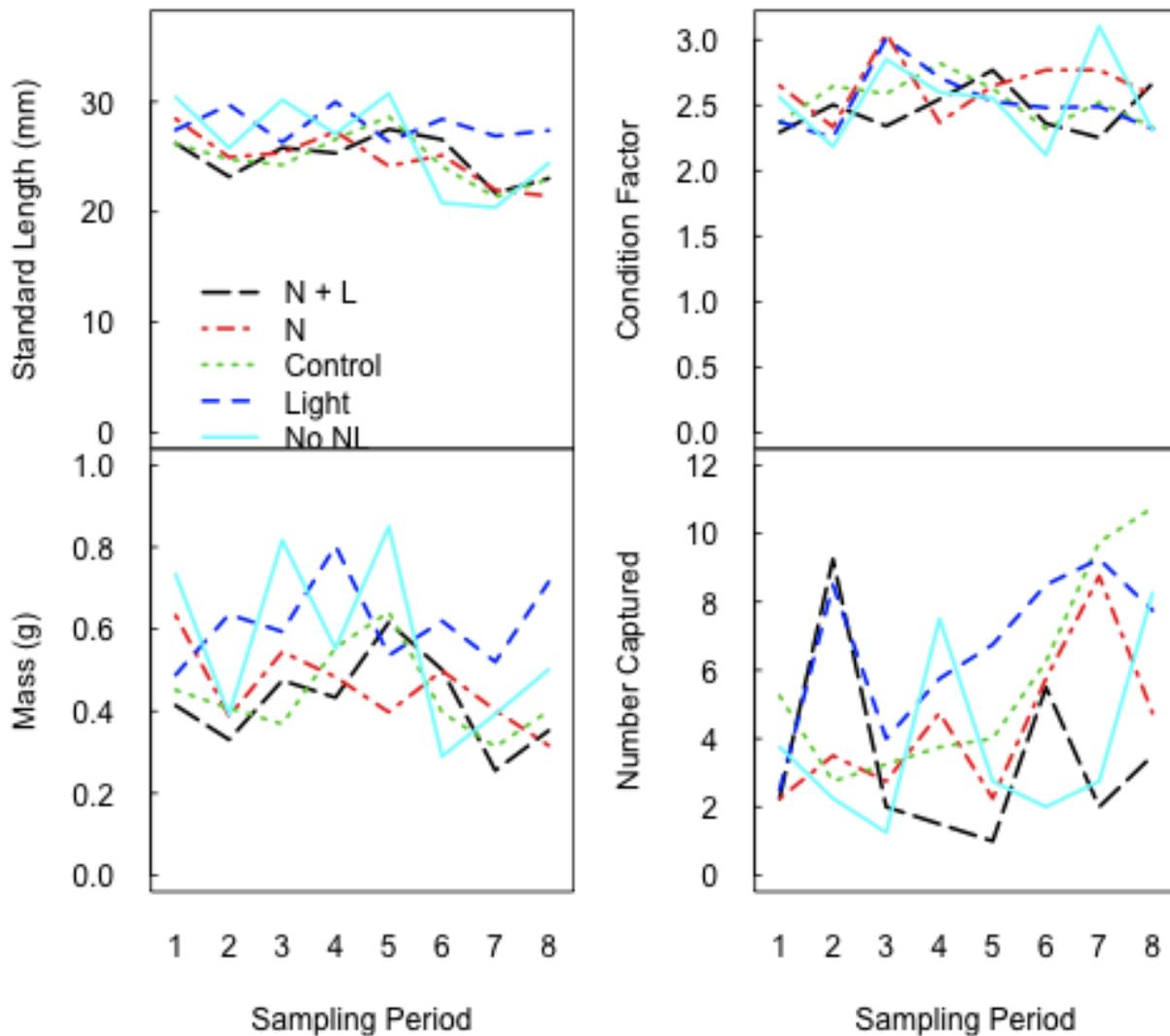


Figure 4-5. Standard length (mm), mass (g), condition factor, and abundance of Sailfin Mollies (*Poecilia latipinna*) captured in minnow traps in plots post-burn in northern Water Conservation Area 3A South of the Everglades, Florida, USA. N+L = Nutrients + Light, N = Nutrients Only, Control = Experimental Control, Light = Light Only, No NL = No Nutrients or Light

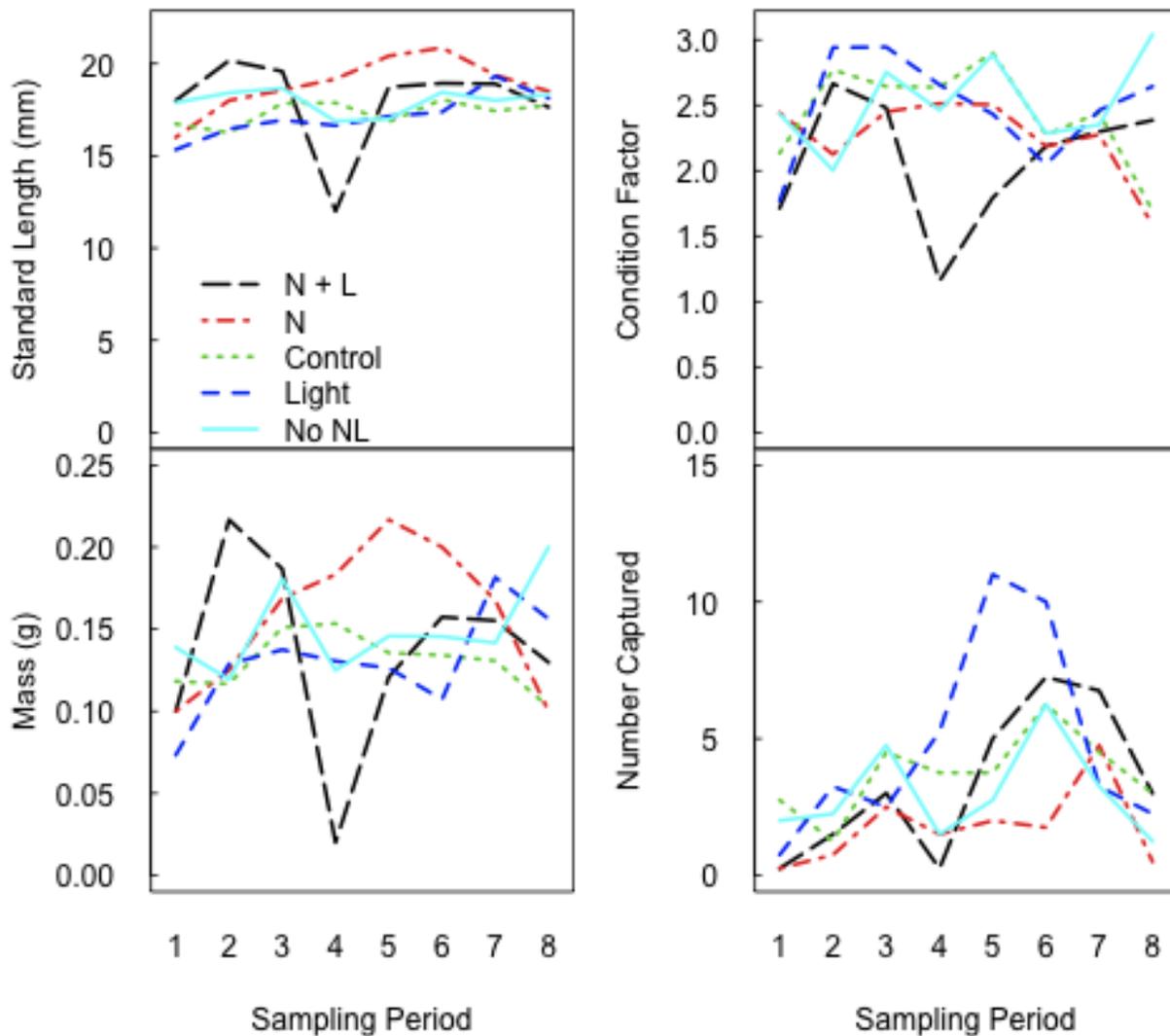


Figure 4-6. Standard length (mm), mass (g), condition factor, and abundance of Least Killifish (*Heterandria formosa*) captured in minnow traps in plots post-burn in northern Water Conservation Area 3A South of the Everglades, Florida, USA. N+L = Nutrients + Light, N = Nutrients Only, Control = Experimental Control, Light = Light Only, No NL = No Nutrients or Light

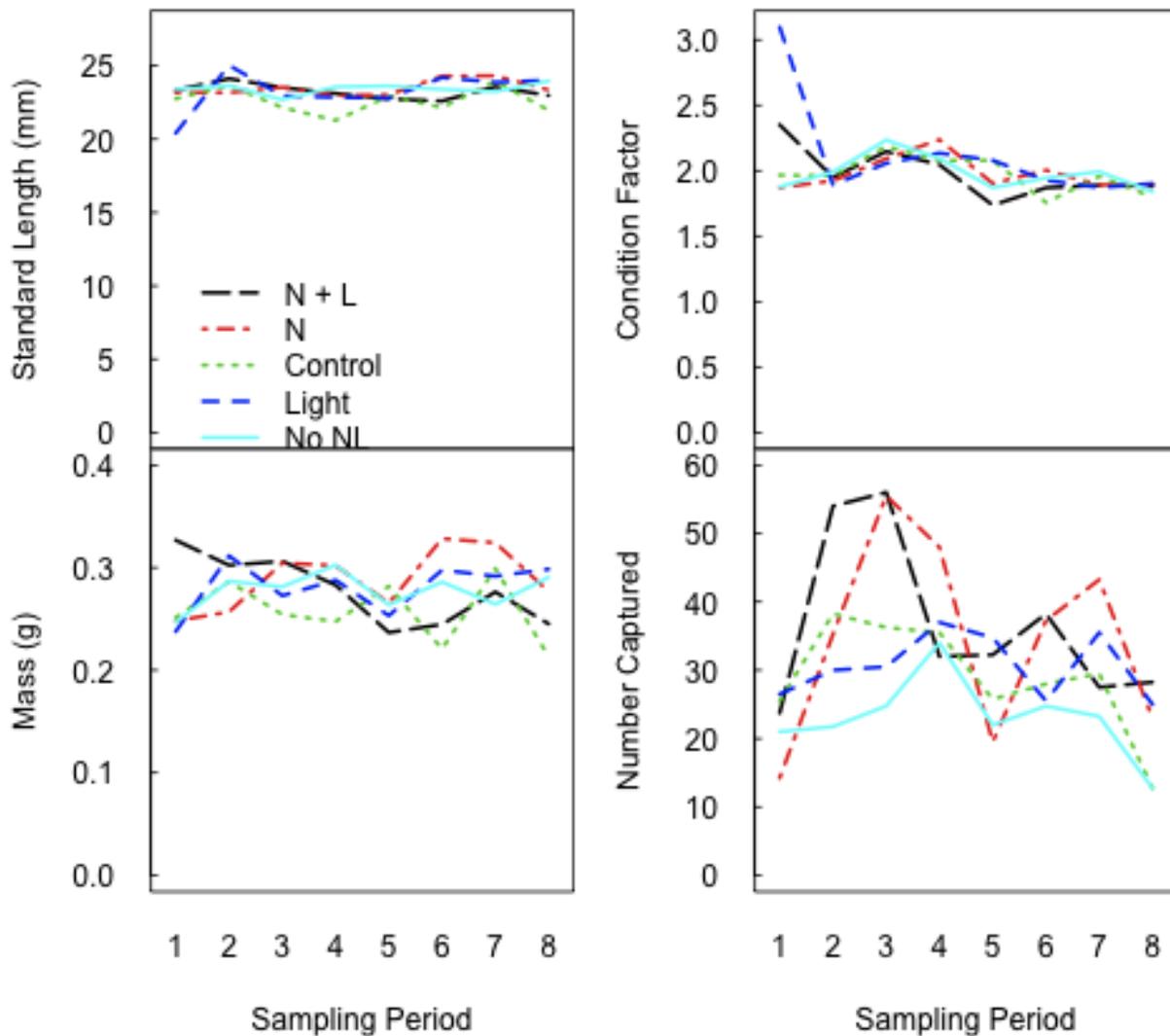


Figure 4-7. Standard length (mm), mass (g), condition factor, and abundance of Eastern Mosquitofish (*Gambusia holbrooki*) captured in minnow traps in plots post-burn in northern Water Conservation Area 3A South of the Everglades, Florida, USA. N+L = Nutrients + Light, N = Nutrients Only, Control = Experimental Control, Light = Light Only, No NL = No Nutrients or Light

CHAPTER 5 CONCLUSIONS

Fire is a natural process in the Everglades, important for recycling nutrients and maintaining vegetative communities. While wildfires typically occur at the onset of the wet season (Slocum et al. 2007), prescribed fires are frequently conducted to reduce fuel loads and manage habitat for wildlife (Marsha Ward, FWC, pers. com.). Frequent fires remove tall, dense stands of sawgrass, opening areas of previously inaccessible, shallow water marsh to foraging wading birds. Prescribed burns are conducted during the dry season when water levels are declining, limiting the length of time these shallow burned areas are available as foraging habitat for wading birds. Areas of shallow water are preferred habitat for wading birds given conditions of similar prey densities (Gawlik 2002). Wading birds preferred burned areas for the first 2-3 weeks post-burn (Chapter 3). Great egrets had higher capture efficiency in these burned sawgrass ridges than in the surrounding sloughs, but had a higher capture rate in sloughs than in burns because they made more strikes. Over multiple weeks post-burn, prey densities do not appear to be greater in burned areas than the adjacent sloughs, suggesting that wading bird preference of burned areas is based on water depth and prey accessibility.

Fish response to burns was limited, despite an increase in P and periphyton biomass. Fish abundance in burns appeared to increase temporarily in response to light and nutrients increased by the burn (Chapter 3). Additionally, select individual fish species increased in size in burns and may increase reproductive output, and thus abundance, of this species. However, sampling of burned ridges indicate that prey densities are lower on recently burned ridges than in sloughs (Chapter 4). Overall, the whole fish community did not increase in size, but did briefly increase in abundance.

From the perspective of a wading bird, changes in the whole fish community are likely a better representation of composite diet that wading birds eat rather than changes of individual species. Thus, prescribed burns do not appear to enhance the caloric intake of wading birds foraging in burns.

These studies add to the limited body of knowledge about fire effects on wetland-dependent wildlife (Chapter 2), expanding our understanding of how fire impacts foraging opportunities and resources for wading birds in the Everglades. The response by wading birds to fire is likely to occur in other wetlands when shallow water areas of marsh are exposed for foraging after a burn. Fire in other wetlands can be expected to release nutrients although the effects of bioavailable nutrients are dependent on the concentration of bioavailable nutrients released and the concentration already available in the wetland. I expect a stronger response by primary producers to nutrient release to occur in oligotrophic wetlands than in nutrient enriched wetlands. However, the primary result of this research is that prey availability, rather than prey biomass, appears to drive the preference foraging wading birds exhibit for burned areas. Changes in season and severity of the fire will alter these responses and should be explored.

APPENDIX A
 WHITE IBIS (*EUDOCIMUS ALBUS*) AND SNOWY EGRET (*EGRETTA THULA*) CAPTURE EFFICIENCIES AND
 CAPTURE RATES

Table A-1. Summary of capture rates and capture efficiencies reported for white ibis (*Eudocimus albus*) and snowy egret (*Egretta thula*) in southern Florida marshes.

Study	Condition	Capture Rate (N)	Capture Efficiency (N)	Location
<i>White ibis</i>				
Surdick (1998)	1996	1.4 (151)		Everglades
	1997	0.6 (219)		
Lantz et al. (2010)	January	0.79-1.02 (71)		SAV ^a density experiment
	April	1.78-2.24 (135)		
This study	2009	1.6 (43)	0.03 (43)	Everglades WCA-3A ^b
	2010	0.74 (18)	0.01 (18)	
<i>Snowy egret</i>				
Surdick (1998)	1996	1.02 (213)		Everglades
	1997	0.6 (206)		
Lantz et al. (2010)	January	0.28-0.53 (35)	0.14-0.30 (33)	SAV density experiment
	April	0.90-1.49 (124)	0.23-0.30 (123)	
Lantz et al. (2011)		0.78-1.35 (92)	0.20-0.41 (89)	Emergent vegetation experiment
This study	2009	1.5 (13)	0.4 (13)	Everglades WCA-3A
	2010	0.12 (5)	0.07 (5)	

^aSubmerged aquatic vegetation

^bWater Conservation Area 3A

Table A-2. Capture rate (captures per minute) and capture efficiency (captures per attempt) of white ibis (*Eudocimus albus*) in 2009 and 2010 in Water Conservation Area 3A of the Everglades, USA.

Variable	2009		2010	
	Burn	Slough adj. Burn ^a	Burn	Slough adj. Burn
Number of observations	5	38	8	10
Mean capture rate (\pm sd)	1.2 (1.3)	1.7 (1.2)	0.67 (0.4)	0.79 (0.6)
Range of capture rate	0-3.2	0-6.8	0-1.2	0-2.2
Mean capture efficiency (\pm sd)	0.03 (0.03)	0.03 (0.02)	0.01 (0.008)	0.01 (0.01)
Range of capture efficiency	0-0.08	0-0.14	0-0.02	0-0.05
Average attempts per minute	38.7 (9.2)	61.7 (13.5)	61.0 (8.9)	55.0 (10.2)
Water depth (cm)	3.0 (3.7)	14.7 (4.1)	8.8 (1.7)	20.9 (3.5)
Range of water depth (cm)	0-9	3-25	7-11	17-27

^aSloughs adjacent to burns

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BIOGRAPHICAL SKETCH

Louise S. Venne grew up in Wisconsin. She attended the University of Wisconsin-Stevens Point where she earned Bachelor of Science degrees in Wildlife and in Chemistry. She then attended Texas Tech University for a Master of Science degree in Environmental Toxicology studying land use effects on amphibian community composition in playa wetlands. After working for a year as an environmental consultant, Louise enrolled in the Department of Wildlife Ecology and Conservation at University of Florida (UF). She was one of the fellows in the National Science Foundation funded Integrative Graduate Education and Research Traineeship programs at UF titled “Adaptive Management: Wise Use of Water, Wetlands, and Watersheds”. Louise received her Ph.D. from the University of Florida in August 2012.