

RESEARCH ARTICLE

FORAGING WADING BIRD (CICONIIFORMES) ATTRACTION TO PRESCRIBED BURNS IN AN OLIGOTROPHIC WETLAND

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ABSTRACT

Many wetland communities are fire prone or fire dependent, especially those dominated by forbs and grasses. Despite our considerable knowledge about fire effects on wildlife in uplands, there is a relative paucity of information about effects of fire in wetland systems. Long-legged wading birds (herons, egrets, ibises, storks, spoonbills; order Ciconiiformes) may benefit from fire through the exposure of prey after vegetation removal, or through a trophic response of prey to increased availability of nutrients and increased light. We conducted aerial surveys of foraging wading birds in prescribed burns and adjacent unburned areas in the central Everglades, Florida, USA, to determine if wading birds select for burned habitats. We measured aquatic prey density in burned and unburned sawgrass (*Cladium mariscus* [L.] Pohl ssp. *jamaicense* [Crantz] Kük), and densities of prey injured or killed in the fires. We also observed foraging great egrets (*Ardea alba* L.) in and adjacent to prescribed burns to determine whether foraging success (i.e., capture efficiency and capture rate) differed between burned and unburned areas. Great egrets and white ibises (*Eudocimus albus* L.) selected for burns and areas of deeper water adjacent to burned areas, and avoided dense, tall, unburned vegetation. Measured densities of prey killed by the fire were very low. Live aquatic prey densities did not differ between burned and unburned sawgrass. Great egrets had higher capture rates in sloughs adjacent to burns than in burned areas, but were more efficient at capturing prey in burned areas than in adjacent sloughs. Prescribed fires created short-term shallow water habitats (burned areas) with limited submerged and emergent vegetation, making prey in burns more vulnerable despite lower densities (availability) compared to adjacent sloughs. This research suggests that prescribed fire in grass-dominated wetlands may attract predators like wading birds primarily because removal of vegetation makes prey easier to capture.

Keywords: *Ardea alba*, capture efficiency, capture rate, *Eudocimus albus*, Everglades, great egret, habitat selection, prey accessibility, prey density, white ibis

Citation: Venne, L.S., and P.C. Frederick. 2013. Foraging wading bird (Ciconiiformes) attraction to prescribed burns in an oligotrophic wetland. *Fire Ecology* 9(1): 78-95. doi: 10.4996/fireecolgy.0901078

INTRODUCTION

Disturbance of upland areas via machinery, fire, and other physical disturbances often attract predatory 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 predatory birds may increase because of improved availability of prey, but not due to increased abundance or diversity of prey (Devereux *et al.* 2006). Disturbances like fire can also affect the abundance and diversity of invertebrates in uplands and in some peatlands in the longer term (Warren *et al.* 1987, Hochkirch and Adorf 2007), although directionality of responses is not consistent among species. While changes in prey availability due to disturbance are known from some upland habitats (e.g., Boyd and Bidwell 2001, Benson *et al.* 2007), it is unclear whether disturbance from fire results in similar 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). Many wetland bird species are not found in recently burned habitat for a year or more, while other species are observed in burns where they were previously not found (Venne 2012). For example, savannah sparrows (*Passerculus sandwichensis*) tend to be found in areas with sparse vegetation within one year post-burn, while sedge wrens (*Cistothorus platensis*) prefer dense vegetation that has not burned in the previous two years (Baldwin *et al.* 2007). However, studies of post-burn responses of wildlife typically have not determined the mechanisms driving avoidance or preference of burned areas. Fire may positively affect foraging conditions for many wetland dependent birds

through nutrient release and resetting vegetation composition, thereby exposing roots and seeds (Gabrey *et al.* 1999), increasing nutritive content in vegetation (Smith *et al.* 1984), and increasing abundance of food resources such as invertebrates (de Szalay and Resh 1997, Hochkirch and Adorf 2007). However, changes in resource availability and quality depend in part on the time of year that the burn is conducted (Brennan *et al.* 2005, McWilliams *et al.* 2007). Also, fire may change patterns of resource availability in wetlands both in the short and long term, which could have management and conservation implications.

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 dense or no emergent vegetation (Lantz *et al.* 2011), and edges may be preferred over open water (Stolen 2006).

The Everglades is a large oligotrophic wetland in southern Florida, USA, where primary production is strongly phosphorus limited (Noe *et al.* 2001). Wading birds are an iconic, abundant group of species and also serve as one of the indicators of restoration of the Everglades (Frederick *et al.* 2009). Sawgrass (*Cladium mariscus* [L.] Pohl ssp. *jamaicense* [Crantz] Kük) is the dominant vegetation, forming elevated, elongate “islands” (i.e., ridges) surrounded by deeper, open water sloughs (Gunderson 1994). Sawgrass is a fire-adapted plant, growing quickly and recovering within two 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 with frequencies of 6 mo to 7 mo, 1 yr, and 10 yr to 14 yr (Gunderson and Snyder 1994). Long-term data from Everglades National Park indicate that there may also be return frequencies of 6 yr and 40+ yr.

Fire is a natural component of this landscape (Wade *et al.* 1980). Fires occur most frequently at the onset of the wet season (May to June) when lightning strikes commonly occur (Gunderson and Snyder 1994, Slocum *et al.* 2007) and when water depths are most shallow. The greatest number of wildfires occurs due to lightning ignitions at the peak of the seasonal thunderstorm pattern in July (Gunderson and Snyder 1994). More acreage is burned by fire during the transition from dry season to wet season in May than at any other time of year. In dry years, wildfires often burn into the peat. In contrast, prescribed fires are conducted by state and federal agencies attempting to mimic fire return intervals, although often not during the same season as natural fires. Prescribed fires frequently are conducted in winter and spring when at least 10 cm of surface water protects the underlying peat layer from ignition. 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.

Fire may therefore 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. In this study, we first tested the general prediction that wading birds select for burned habitats over unburned habitat (H1). We also examined several mechanisms that might explain why birds are attracted to burns. We 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 (H2). Under the assumption that primary production post burn would be elevated, we also tested the prediction that live prey densities would be greater in burned than unburned sawgrass (H3). If gross reductions in vegetation create higher prey vulnerability, we predicted that wading birds would have a higher capture rate (captures per minute; H4a) and capture efficiency (captures per attempt; H4b) in burned areas than in unburned areas, accounting for effects of water depth, flock size, and time since burn.

METHODS

We conducted this study in the central and northern portion of Water Conservation Area 3A South of the Everglades (N 25° 54' to 26° 9', W 80° 30' to 80° 48'), Florida, USA. In 2009 and 2010, the Florida Fish and Wildlife Conservation Commission (FWC) conducted three burns each year in Water Conservation Area 3A South of the Everglades as part of their management plan to burn these areas approximately every five years. Burn history varied for each of the areas depending on weather and fuel conditions, and manpower available (Table 1). We used these six burns as treatments for effects of fire on foraging success of wading birds, only in the year burned (Figure 1; Table 1). We used an additional prescribed burn (Apple Camp) conducted in 2011 to sample prey. These burns ranged from 548 ha to 1039 ha and were composed of approximately 67% to 85% sawgrass (Table 1). Fuel density classes, determined by visual estimates of sawgrass densities, were recorded by FWC personnel. All prescribed burns used for this study occurred in a given year within a six-week period from 16 February until 1 April. At the time of the burns, minimum estimated water depths ranged from 10 cm to 30.5 cm on the sawgrass ridges.

Table 1. Description of conditions under which prescribed burns were conducted by the Florida Fish and Wildlife Conservation Commission in Water Conservation Area 3A that was used for wading bird foraging observations and prey studies in 2009 through 2011.

Burn ^a	Heat N Smoaks ^b	Jessie's Holiday ^b	Lost Lemon ^b	Hackberry East ^{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	3 Mar 10	1 Apr 10	2 Mar 11
Size (ha)	1003	931	1039	817	548	690	884
Yr last burned ^e	2004	2005	2005-W	2007-E	2006	1997-N 2006-W	2005
Weather conditions							
Dispersion	45	62	70	60	48	42	55
Min. mixing ht (m)	914	1219	1524	823	823	NA	1219
Estimated % habitat composition							
Sawgrass	70	70	85	70	75	70	67
Slough	14	19	7	29	13	25	15
Other	16	11	8	1	12	5	18
Estimated fuel density (%) ^a							
Light	30	30	20	40	20	20	15
Moderate	50	55	70	40	25	35	15
Heavy	20	15	10	10	55	45	70
Fine fuel moisture	NA	10	NA	8	8	8	9
Onsite conditions							
Water depth (cm)	10 to 18	18 to 25	10 to 20	30	10 to 30	10	15 to 20
Time collected	1055	1010	1110	1200	0900	0950	1049
Wind (m s ⁻¹ ; \bar{x} /max)	NE 2.2/4.0	NE 2.7/4.0	SE 4.0/7.2	NW 3.1	W 2.4/4.0	NE 0.5/1.4	NE 4.9
Relative humidity (%)	60	61	62	52	75	80	60
Air temperature (°C)	22.2	23.9	27.2	17.8	12.8	19.4	26.7
Flame length (m)	2.1		2.4 to 3.0	1.2 to 3.0			0.91 to 4.6
ROS (m min ⁻¹)				0.61			

^a Data taken from burn prescriptions provided by FWC. Estimated fuel density is visual quantification of sawgrass density (main fuel).

^b Burn used for wading bird foraging observations.

^c Burn used for pre- and post-burn prey quantification.

^d Burn used for comparison of prey densities.

^e W, E, and N designate burn occurred in west, east, and north portion, respectively, of burn unit in year listed. NA = not available.

Foraging Habitat Selection

In 2009 and 2010, we surveyed aerial transects (eight transects in 2009 and five in 2010) to cover 100% of the three prescribed burn units burned each year and an equivalent adja-

cent area at the same latitude that would remain unburned (Figure 1). Transects were oriented east-west and separated by 1.33 km. All areas were surveyed weekly for 8 to 10 weeks until the sloughs dried or the wading birds dispersed. We flew transects with two observers

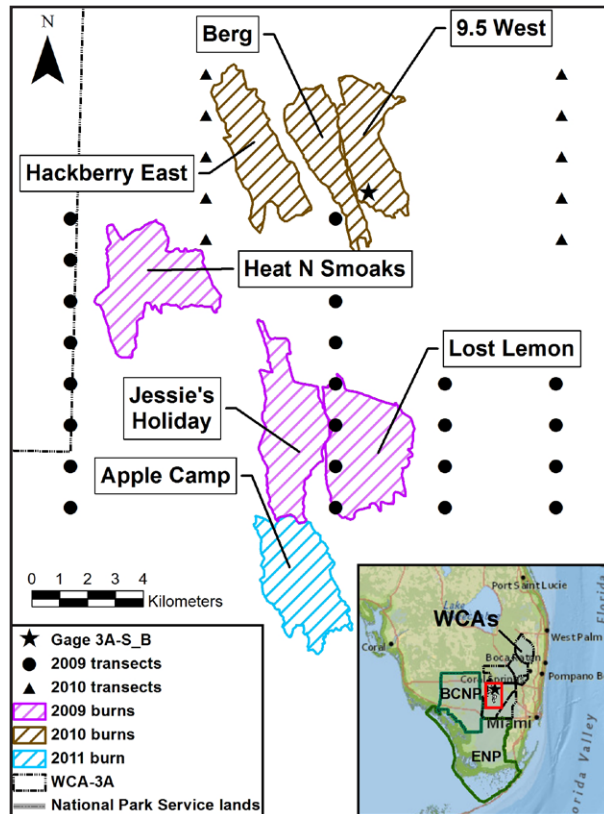


Figure 1. Study area including prescribed burns conducted in 2009 through 2011 that were used in various components of this study. The 2009 (Heat N Smoaks, Jessie’s Holiday, Lost Lemon) and 2010 burns (9.5 West, Hackberry East, Berg) were used for flight surveys and foraging observations, and the 2010 burns were also used for injured or killed prey item surveys. The 2011 burn (Apple Camp) was used for aquatic prey density. ENP = Everglades National Park, BCNP = Big Cypress National Preserve, and WCA = Water Conservation Area

looking out opposite sides of a fixed-wing Cessna 182 at velocities of 185 km h⁻¹ to 222 km h⁻¹, and at 244 m in altitude, an elevation at which foraging, white wading birds are recognizable by shape, size, and behavior. We recorded species, number of individuals, and habitat in which white, foraging wading birds were observed. Habitat categories were Grass (unburned sawgrass with a few shrubs), Burn (burned sawgrass), Slough, Sloughs Adjacent to Burns, and Track (i.e., trails created by airboats). Sloughs Adjacent to Burns were iden-

tified visually based on the presence of a blackened burn area adjacent to the slough from photographs taken from 305 m to 610 m altitude within one week post burn during surveys. When groups of birds were more than six, the observer took 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, we categorized them as white wader so that species with differing foraging habits were not miscategorized.

We digitized the area of Burn using Digital Orthophoto Quarter Quads (DOQQs) from 2003 in ArcGIS based on photographs of the burn taken as soon as possible post burn during flights from 305 m to 610 m altitude. Using GIS, we calculated area of each digitized patch in each burn. Since airboat tracks constituted linear depressions that were often attractive to wading birds, we 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 we used the clip function in ArcGIS to determine vegetation types in survey areas and burn units to determine area of Sloughs Adjacent to Burns using vegetation polygons determined by Rutchey *et al.* (2005). We subtracted Track area (approximately 80% through grass and 20% through slough) from Grass and Slough since burned areas were digitized to exclude tracks. We lumped the very detailed vegetation classifications from Rutchey *et al.* (2005) to match our broad habitat categories, and calculated area of each of our habitat categories: Burn, Grass, Tree Island, Slough, Sloughs Adjacent to Burns, and Track. Calculated area of burn and slough type changed when each additional burn was conducted. We used water level over the period of aerial surveys at gaging station 3A-S_B (Figure 1) to capture water depth trends within the study area (SFWMD 2012).

Prey Item Survey

During 2010, we surveyed 25 randomly selected locations in sawgrass in each of the three burn units for injured or dead biota that could serve as prey items for wading birds. A set of random points (i.e., 50 to 100) was generated in ArcGIS within each burn border, and we used points only in sawgrass that were no more than 200 m from the edge of the slough. We 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. At each location, we recorded water depth and maximum vegetation height, and two people searched within a 0.5 m radius for potential prey items preburn and post burn. We searched in the water and among burned sawgrass culms, but did not count live fish since our presence disturbed these species.

Aquatic Prey Density

We used a 1 m² aluminum-sided throw trap to sample aquatic prey within an approximately 884 ha prescribed burn and an area of similar size immediately adjacent to the prescribed burn to compare habitats with similar water depths. The area of unburned sawgrass was east and adjacent to the prescribed burn. Of the other two prescribed burns conducted in 2011, one was dry before sampling began and the other unit did not burn sufficiently due to deeper water depths to be comparable to the other prescribed burns sampled. The prescribed Apple Camp burn was conducted on 2 March 2011 (Figure 1) over minimum water depths of 15 cm to 20 cm. Starting one day post burn, we measured small fish and macroinvertebrate density and environmental characteristics at randomly generated points in burned and adjacent unburned sawgrass ridges. We threw three throw traps in each sampling location and removed vegetation to facilitate clearing of traps. We 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, we measured water depth, vegetation height, estimated percent periphyton cover to the nearest 5%, and counted sawgrass stems. At each sampling point with adequate water depths (≥ 10 cm), we set 3 Gee minnow traps (23 × 45 cm, 3.2 mm mesh, Memphis Net & Twine Co., Inc., Memphis, Tennessee, USA) for two hours. After the two hours, we collected and preserved all aquatic organisms captured. Organisms that were too large for 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 millimeter.

Foraging Observations

We observed 104 foraging great egrets (*Ardea alba*) in Burns and Sloughs Adjacent to Burns from a 6.5 m tower mounted on an airboat at 54 locations post burn in 2009 and 2010. We 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 (5 min to 15 min). We terminated observations if the bird walked out of sight, flew away, or at the end of the observation time. We counted successful and unsuccessful striking attempts; and recorded number of individuals of each species in a flock, water depth, and coordinates of the foraging location. When observing a flock, we observed as many birds in each flock as possible until the birds flew away or we could no longer ensure that we were observing an identifiable new bird.

Statistical Analysis

We calculated Manly's habitat selection ratio for great egrets and white ibis (*Eudocimus*

albus L.) in each year following Manly *et al.* (2002). We used great egrets and white ibises because foraging individuals of these two species are readily detected, identified, and counted from the air. A selection ratio of 1 indicates habitat use is in direct proportion to habitat availability. Selection ratios <1 indicate avoidance, while selection ratios >1 indicate selection for the habitat. We compared selection ratios in each habitat type to calculated expected use via a chi-squared analysis and calculated 95% confidence limits using the Bonferroni correction (Manly *et al.* 2002).

Due to the low number of potential prey items found, no statistical analyses were performed on data collected during the prey item survey; however, densities of potential prey are indicative of whether prey items killed or injured during the fire are sufficient to attract wading birds. From samples of aquatic prey collected with a 1 m² throw trap, we checked normality of environmental variables (i.e., water depth, sawgrass stem and total stem density, vegetation height, and percentage periphyton and vegetation cover), density of aquatic organisms (i.e., fish, crayfish [*Procambarus* spp.], grass shrimp [*Palaemonetes paludosus* {Gibbes, 1850}], amphibians, and aquatic invertebrates [>5 mm total length]), and length of aquatic organisms (fish and crayfish). We 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 standard length of fish 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 transformed to fit a normal distribution, and we used a Kruskal-Wallis rank sum test to test for differences between burned and unburned sawgrass.

We constructed models of capture rate (number of captures per minute) 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. We 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 the number of zeroes in the data set. We constructed models 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. The number of birds within a foraging flock affects foraging success of wading birds (Krebs 1974), so we controlled for flock size 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 we included time since burn as a covariate to describe the effect that this variable has on foraging success of wading birds. We 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). We re-scaled AIC_c values (Δ_i) based on the AIC_c value of the best model (i.e., lowest AIC_c value), and calculated weighted values (w_i). We reported coefficients for all models with $\Delta_i < 2$. Percent deviation (% D) was calculated from the null and residual deviances (i.e., % D = (null – residual) ÷ null) for models of capture rate and capture efficiency. All statistical analyses were performed using R 2.10.1 (R Development Core Team 2009).

RESULTS

Foraging Habitat Selection (H1)

Great egrets had a high selection ratio for Burns in the first two weeks (approximately 3.5 weeks after the first burn) of the surveys in

2009 (Table 2). In 2010, great egrets similarly showed selection for Burns for more than two weeks post burn (Table 2). Great egrets avoided burns when there was no standing water in the burn (e.g., mid-March). Great egrets only selected for Burns in proportion to the availability of burned areas in the survey area immediately after the third prescribed burn on 27 March 2009, and for the last four surveys in 2010 (Table 2). Conversely, great egrets strongly avoided unburned Grass in both years (Table 2). Much of the use of unburned sawgrass by great egrets occurred in thin strips of sawgrass between Burn and Sloughs Adjacent to Burns. In 2009, the selection ratio for Sloughs Adjacent to Burns increased as water

levels declined (Table 2). Great egrets typically used Tracks substantially more than available.

White ibises 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 (Table 3). White ibises generally selected for both slough types in both years more than their availability. Conversely, white ibises strongly avoided unburned Grass stands in both years, and in 2010, were not observed in one to all habitat types during surveys (Table 3). Ibises strongly selected for Track in 2009 when water levels had receded the most, but only briefly used Track in 2010 when wa-

Table 2. Habitat selection ratios (Bonferroni adjusted 95% confidence interval) for great egrets (*Ardea alba*) in 2009 and 2010 in Water Conservation Area 3A of the Everglades, USA. Prescribed burns in 2009 were conducted on 17 Feb, 26 Feb, and 27 Mar, and in 2010 on 16 Feb, 03 Mar, and 01 Apr.

Survey Date	Sloughs Adjacent to Burns	Burn	Grass	Slough	Track
2009					
28 Feb	0.718 (0.18 to 1.26) ^{ns}	2.985 (2.03 to 3.94)	0.265 (0.13 to 0.40)	1.019 (0.75 to 1.29) ^{ns}	54.44 (34.84 to 74.04)
6 Mar	0.761 (0.36 to 1.17) ^{ns}	3.200 (2.49 to 3.91)	0.262 (0.16 to 0.36)	1.273 (1.07 to 1.48) ^{ns}	28.16 (17.22 to 39.09)
12 Mar	2.217 (1.75 to 2.68)	1.934 (1.51 to 2.36)	0.052 (0.03 to 0.08)	1.866 (1.75 to 1.98)	24.22 (17.83 to 30.60)
20 Mar	0.712 (0.50 to 0.93) ^{ns}	0.407 (0.25 to 0.57)	0.024 (0.01 to 0.04)	2.191 (2.09 to 2.29)	41.16 (34.20 to 48.11)
28 Mar	2.274 (1.78 to 2.77)	0.753 (0.49 to 1.02) ^{ns}	0.019 (0.00 to 0.04)	1.764 (1.60 to 1.93)	43.83 (33.04 to 54.63)
3 Apr	4.080 (3.67 to 4.49)	0.230 (0.13 to 0.33)	0.041 (0.02 to 0.06)	1.346 (1.23 to 1.46)	51.21 (43.36 to 59.06)
10 Apr	0.935 (0.75 to 1.12) ^{ns}	0.005 (0.00 to 0.02)	0.016 (0.01 to 0.03)	2.624 (2.55 to 2.70)	24.25 (19.65 to 28.85)
2010					
15 Feb	NA	NA	0.154 (0.05 to 0.26)	2.434 (2.16 to 2.71)	20.99 (6.77 to 32.21)
26 Feb	1.486 (0.53 to 2.44) ^{ns}	1.775 (0.77 to 2.78) ^{ns}	0.540 (0.41 to 0.67)	1.830 (1.55 to 2.11)	1.673 (0.00 to 4.71) ^{ns}
5 Mar	2.095 (1.45 to 2.74)	2.898 (2.30 to 3.50)	0.479 (0.39 to 0.57)	1.249 (1.04 to 1.46) ^{ns}	4.366 (0.85 to 7.88)
13 Mar	2.401 (1.60 to 3.20)	0.543 (0.20 to 0.89) ^{ns}	0.253 (0.17 to 0.34)	2.325 (2.07 to 2.58)	8.977 (3.14 to 14.82)
19 Mar	3.213 (2.25 to 4.17)	0.386 (0.08 to 0.67) ^{ns}	0.046 (0.00 to 0.09)	2.644 (2.39 to 2.90)	8.167 (2.21 to 14.12)
25 Mar	2.349 (1.45 to 3.25)	0 ^a	0.026 (0.00 to 0.06)	2.989 (2.75 to 3.22)	9.188 (2.51 to 15.87)
31 Mar	2.394 (1.39 to 3.40)	0.971 (0.41 to 1.54) ^{ns}	0.120 (0.04 to 0.20)	1.899 (1.57 to 2.23)	40.89 (26.49 to 55.29)
8 Apr	2.836 (1.99 to 3.68)	0.868 (0.42 to 1.32) ^{ns}	0.063 (0.00 to 0.12)	2.385 (2.01 to 2.76)	7.934 (0.85 to 15.02)
15 Apr	2.747 (1.90 to 3.59)	0.768 (0.34 to 1.20) ^{ns}	0.064 (0.00 to 0.13)	2.463 (2.09 to 2.84)	8.127 (0.87 to 15.38)
25 Apr	2.486 (1.42 to 3.55)	1.155 (0.49 to 1.82) ^{ns}	0.185 (0.05 to 0.32)	2.122 (1.63 to 2.62)	6.828 (0.00 to 15.48)

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

NA = not available; this survey occurred preburn.

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

Table 3. Habitat selection ratios (Bonferroni adjusted 95% confidence interval) for white ibis (*Eudocimus albus*) in 2009 and 2010 in Water Conservation Area 3A of the Everglades, USA. Prescribed burns in 2009 were conducted on 17 Feb, 26 Feb, and 27 Mar, and in 2010 on 16 Feb, 03 Mar, and 01 Apr.

Survey Date	Sloughs Adjacent to Burns	Burn	Grass	Slough	Track
2009					
28 Feb	2.567 (1.97 to 3.17)	3.476 (2.83 to 4.12)	0.235 (0.15 to 0.32)	1.123 (0.94 to 1.30) ^{ns}	0 ^a
6 Mar	2.165 (1.77 to 2.56)	1.801 (1.45 to 2.16)	0.432 (0.36 to 0.51)	1.365 (1.24 to 1.49)	2.737 (0.52 to 4.95) ^{ns}
12 Mar	3.071 (2.74 to 3.40)	1.979 (1.71 to 2.25)	0.097 (0.08 to 0.12)	1.795 (1.72 to 1.87)	9.960 (7.33 to 12.59)
20 Mar	0.591 (0.43 to 0.75)	0.544 (0.40 to 0.69)	0.217 (0.18 to 0.26)	2.259 (2.18 to 2.34)	13.32 (9.88 to 16.76)
28 Mar	1.417 (1.13 to 1.71)	1.792 (1.52 to 2.06)	0.008 (0.00 to 0.02)	1.920 (1.80 to 2.04)	19.70 (14.34 to 25.07)
3 Apr	6.151 (5.67 to 6.64)	0 ^a	0.050 (0.02 to 0.08)	0.855 (0.74 to 0.97) ^{ns}	51.14 (42.27 to 60.00)
10 Apr	2.231 (1.89 to 2.57)	0 ^a	0.013 (0.00 to 0.03)	2.462 (2.36 to 2.56)	8.456 (4.93 to 11.98)
2010					
15 Feb	NA	NA	0.271 (0.13 to 0.41)	2.428 (2.13 to 2.73)	5.529 (0.00 to 13.64) ^{ns}
26 Feb	6.443 (5.26 to 7.62)	5.159 (4.11 to 6.21)	0.264 (0.20 to 0.33)	1.226 (1.04 to 1.41) ^{ns}	0.745 (0.00 to 2.10) ^{ns}
5 Mar	1.168 (0.92 to 1.41) ^{ns}	5.410 (5.07 to 5.75)	0.099 (0.08 to 0.12)	1.553 (1.45 to 1.66)	0 ^a
13 Mar	2.156 (1.51 to 2.80)	2.416 (1.86 to 2.97)	0.011 (0.00 to 0.03)	2.464 (2.26 to 2.67)	0 ^a
19 Mar	2.774 (1.96 to 3.59)	0.563 (0.23 to 0.90) ^{ns}	0.070 (0.02 to 0.12)	2.785 (2.57 to 3.00)	0 ^a
25 Mar	0 ^a	0.192 (0.00 to 0.47) ^{ns}	0.048 (0.00 to 0.10)	3.584 (3.44 to 3.73)	0 ^a
31 Mar	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a
8 Apr	4.061 (0.00 to 8.84) ^{ns}	5.179 (1.53 to 8.83)	0 ^a	0 ^a	0 ^a
15 Apr	0.241 (0.00 to 0.85) ^{ns}	7.182 (6.10 to 8.26)	0.083 (0.00 to 0.23)	0.283 (0.00 to 0.69) ^{ns}	0 ^a
25 Apr	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a

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

NA = not available; this survey occurred preburn.

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

ter levels were dropping. Water levels dropped steadily from 13 February 2009 until 18 March 2009, approximately 4 mm day⁻¹, with one increase of 40 mm in water depth over two days before dropping at 6 mm day⁻¹ (SFWMD 2012). In 2010, water levels initially were very variable with three short periods of dropping water levels (~2.7 mm day⁻¹) before a substantial increase of 110 mm over 5 days at the end of March, and then three changes in water levels, all dropping at approximately 4 mm day⁻¹ from 30 March through the end of surveys on 25 April.

Prey Item Survey (H2)

In pre-burn surveys, we found six possible prey items, all spiders, in a total of 6 of 50 sampling points (0.15 items m⁻²). Mean water depths pre-burn were 8.5 cm in the Berg burn and 14.5 cm in the 9.5 West burn, with water depths at individual sampling locations ranging from 0 cm to 22 cm, representative of the other burns. Surveys immediately after the burn (1 day post burn) yielded nine prey items in a total of 7 of 75 points (0.12 items m⁻²). 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 in a total of 10 of 75 points (0.22 items m⁻²; three worms and two millipedes within sawgrass culms, five spiders, one unidentified invertebrate, and two snails: one live, one dead). Mean water depths ranged from 6.9 cm to 24.3 cm post burn with a range of 0 cm to 31 cm at individual sampling locations. Most of these invertebrates were too small to be wading bird prey items, and were scarce and very well hidden.

Aquatic Prey Density (H3)

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 ($t = -3.02$, $df = 21.7$, $P = 0.01$), suggesting that we inadvertently selected slightly deeper water locations to sample unburned sawgrass. As expected, vegetation height was significantly shorter ($t = -15.1$, $df = 18.5$, $P < 0.01$) in burned than unburned sawgrass. Stem density was significantly greater in unburned than burned sawgrass plots ($t = -2.12$, $df = 22.7$, $P = 0.05$), probably 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 was significantly greater ($t = -2.39$, $df = 27.8$, $P = 0.02$) in unburned than in burned sawgrass. Percent periphyton cover was significantly greater ($t = -2.79$, $df = 27.5$, $P = 0.01$) in unburned than in burned sawgrass. Density and sizes of most potential prey items did not differ between burned and unburned sawgrass (Venne 2012). In throw trap samples, amphibians (Peninsula newt [*Notophthalmus viridescens piaropicola*], siren [*Siren lacertina*], tadpoles, and adult Florida cricket frog [*Acris gryllus dorsalis*]) were at a significantly higher density (Kruskal-Wallis chi-squared = 6.46, $df = 1$, $P = 0.01$) in burned than unburned sawgrass. Density of aquatic invertebrates (identified to lowest taxa

possible: Belostomatid, Dysticid, Hirudinea, Odonata, Oligochaeta, and creeping water bugs [*Pelocoris femoratus*]) did not differ among treatments.

Foraging Observations (H4a and H4b)

We observed a total of 104 foraging great egrets in 2009 and 2010. Capture rate of great egrets ranged from 0 captures minute⁻¹ to 3.2 captures minute⁻¹ with a mean of 0.43 captures minute⁻¹ across both years and all foraging locations. Water depths at foraging locations were deeper in 2010 than in 2009 in Sloughs Adjacent to Burns (Table 4). In 2009, water levels receded during the sampling period until no surface water was available in Sloughs Adjacent to Burns in the study area, and we conducted no foraging observations 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 foraging observations on 30 March.

The best model of great egret capture rate included flock size, days since burn, habitat, water depth, and flock composition (Appendix 1). Percent deviance of the best model was 26.9%. Great egret capture rate was greater in Sloughs Adjacent to Burns than in Burn (Table 4). 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 Burn, but was negatively related to water depth in Sloughs Adjacent to Burns. Days since burn was positively related to capture rate. 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 5).

Capture efficiency (captures per strike) of great egrets ranged from 0 captures per attempt to 1 capture per attempt, with a mean of 0.39

Table 4. Capture rates (captures per minute) and capture efficiencies (captures per attempt) of great egrets 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 to 0.9	0 to 3.2	0 to 0.4	0 to 0.8
Mean capture efficiency (\pm SD) ^b	0.46 (0.4)	0.38 (0.3)	0.18 (0.3)	0.45 (0.4)
Mean attempts per minute (\pm SD)	0.6 (0.5)	1.3 (1.2)	0.3 (0.3)	0.5 (0.4)
Water depth (cm) (\pm SD)	12.1 (8.9)	16.5 (4.6)	13.9 (4.9)	22.7 (4.4)
Range of water depth (cm)	0 to 21	8 to 25	7 to 21	14 to 30
Mean days since burn (\pm SD)	9.9 (7.8)	18.3 (11.4)	12.1 (13.4)	21.3 (7.5)
Range of days since burn	2 to 28	2 to 36	1 to 27	12 to 28
Mean flock size (\pm SD)	19 (17)	44 (33)	21 (17)	8 (14)
Range of flock size	3 to 60	1 to 111	1 to 46	1 to 48

^a Sloughs Adjacent to Burns

^b Capture efficiencies ranged from 0 to 1.

Table 5. Coefficients, stated as effect size (SE), of generalized linear models of great egret capture rate (Rate) and capture efficiency (Efficiency). The top model of Rate was selected using corrected Akaike's Information Criteria (AIC_c). The two top models of Efficiency were selected using corrected quasi-AIC (QAIC_c).

Variable	Intercept	Depth	Flock size	Flock composition single sp.	Habitat 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 $\Delta AIC_c < 2$; Appendix 1 and models with $\Delta QAIC_c < 2$; Appendix 2.

^aBSL = Sloughs Adjacent to Burns, dSB = days since burned, D*Hab = interaction of depth and habitat, Δ = difference of AIC_c value between best model and the given model.

^b Models of capture rate use a gamma distribution and capture efficiency models use a quasibinomial distribution. Models of capture rate are (capture rate + 0.01) = (explanatory variables) because zeroes cannot be log-transformed.

captures per attempt (Table 4). Capture efficiencies in this study fell within the range of other studies of great egrets in the Everglades (Surdick 1998; Sizemore 2009; Lantz *et al.* 2010, 2011). The models that best explained capture efficiency included flock size, flock composition, habitat, days since burn, and wa-

ter depth (Appendix 2). One of the top two models ($\Delta QAIC_c < 2$) included an interaction term 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_c for each additional term 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 5). Capture efficiency decreased with days since burn in Sloughs Adjacent to Burns.

DISCUSSION

We predicted that wading birds preferred burned over unburned areas (H1). Indeed, wading birds selected recently burned areas in greater proportion than available for a number of weeks post burn. The removal of above-water vegetation by fire exposed shallower sawgrass ridges (Loveless 1959). Sawgrass on these ridges grows in dense, tall (mean: 0.8 m to 1.5 m, but up to 3 m) stands (Gunderson 1994) that can inhibit movement and visibility for large animals such as wading birds. Great egrets and white ibises generally avoid areas of dense vegetation (Hoffman *et al.* 1994), and we believe that the removal of sawgrass by fire allowed wading birds to access these areas. Sawgrass starts growing almost immediately after a fire, but it is unlikely that it grew enough during the ≤ 8 weeks post fire to inhibit wading bird foraging. Shallow water depths are preferred by foraging wading birds given similar prey densities (Gawlik 2002), and shallow water may be one of the primary attractants for birds. Not only did wading birds show a preference for burned areas, but they also remained in these areas over multiple weeks. Our observations suggest that the birds only stopped foraging in burned areas when water levels dropped below the marsh surface and became too low for the birds to use these burned areas.

Tracks provide a linear, limited additional habitat on the landscape that wading birds select for more than any other habitat. Through repeated use by airboats, vegetation growth is

limited and tracks become deeper, thereby retaining water in any given area longer than most of the surrounding marsh. White ibises heavily used tracks when water levels dropped initially in 2010, likely when leg length no longer limited their use of this habitat. Conversely, when water levels rose, great egrets used this habitat preferentially over other areas until prescribed burns were conducted. Wading birds may be responding to availability of prey such as fish. Fish density is often higher in areas adjacent to deep water habitats such as alligator holes and canals than in shallow marsh areas, particularly when water levels decrease as the dry season progresses (Loftus and Kushlan 1987, Rehage and Trexler 2006). Airboat tracks, which are typically deeper than the surrounding sloughs, may function similarly to increase density and, potentially, size class of fish. These tracks may also be a conduit for fish movement to recolonize the marsh after a drydown. Rehage and Trexler (2006) found that when small fish density differed between airboat tracks and the adjacent marsh, densities were greater in the tracks. Similarly, macroinvertebrate density was greater in airboat tracks than in adjacent marshes. Airboat tracks may serve as important hotspots of food resources for wading birds.

We found little evidence that birds are attracted to fires because of abundant prey that are injured or killed by fire (H2). The densities we found on prey item surveys were far below the levels usually associated with wading bird foraging. The lack of injured and dead 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 fire (Whelan 1995). Instead, many small animals 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). Given that prescribed fires in the Everglades are typically conducted with water above the

soil surface, many aquatic and semi-aquatic animals can take refuge in the water. Thus, like in uplands, it appears that fires in herbaceous wetlands result in relatively few dead prey resources post burn.

We had predicted that aquatic prey density would be higher in burned than unburned sawgrass (H3). Fish densities in burned and unburned sawgrass did not differ, suggesting that burning did not affect fish density in sawgrass; however, amphibian density was greater in burned than unburned sawgrass. Burned sawgrass may provide greater visibility to calling anurans due to the removal of dense overstory vegetation, while still providing some cover within the stubble. Also, if burns increase abundance of small invertebrates, anurans and newts may also find enhanced foraging opportunities in burned habitats. Although amphibians generally do not compose a substantial portion of the diet of great egrets, these birds may be opportunistic about switching between available prey (McCrimmon *et al.* 2011). Fish densities on sawgrass ridges in this study were typically lower than densities quantified in sloughs in the Everglades (Loftus and Eklund 1994, Jordan 1996, Jordan *et al.* 1997b, Trexler *et al.* 2002, Williams and Trexler 2006). Densities of fish on burned ridges in this study may have been affected by dropping water levels. We were forced by low water levels to collect the majority of samples near the edge of the ridges due to no standing water farther onto the ridge. Fish density or fish assemblage composition on these edges thus may have been biased by emigration of fish and other prey avoiding desiccation on the ridge. However, Jordan (1996) found lower densities of fish in sawgrass than in sloughs, so fish densities in this study are likely representative of the prey available to wading birds foraging in areas of burned sawgrass just before the burns have no standing water. Although fish densities appear to be lower on burned ridges than in adjacent sloughs, wading birds still chose to forage in the shallower habitats.

Contrary to our prediction (H4a), 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 ranges observed in other areas of the Everglades (Surdick 1998, Lantz *et al.* 2010, 2011, Sizemore and Main 2012), although capture rates in 2010 were at the low end of those reported. 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 been too deep for foraging (Powell 1987, Gawlik 2002).

Despite lower prey densities, capture efficiency was greater in burns than in Sloughs Adjacent to Burns (H4b). 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 in Sloughs Adjacent to Burns is compatible with the prediction that wading birds select burned ridges over sloughs. Burned areas have less submerged aquatic vegetation than sloughs, and almost no thick periphyton mat (L.S. Venne, University of Florida, personal observation; McCormick *et al.* 1998) within the water column. This presumably provides less cover for fish and may enhance the ability of predators to see and capture prey as was noted in studies of invertebrates in grassland habitats (e.g., Devereux *et al.* 2006).

In conclusion, burned sawgrass ridges provided shallow areas that wading birds preferred in comparison to unburned areas, and to areas of deeper water that typically have higher prey densities. However, the strong preference for tracks suggests that some areas of deeper water may be preferential, even more than shallow burned areas. This illustrates dramatically that foraging by wading birds in

this wetland is strongly constrained by the presence of dense sawgrass strands. However, the attraction of open space is clearly also dependent upon water depth, and both open space and shallow depths appear to be necessary to attract wading birds. This mechanism is supported by the fact that birds could forage efficiently in these habitats. We 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. In addition, scavenging would probably end in a few days following the fire due to decomposition of the injured and dead prey, whereas the birds continued to be attracted to burns for up to 3 weeks post burn. While burning did not appear to change the densities of fishes, burning may increase the densities of amphibians. Whether this increase in amphibians is enough to help drive the attraction of birds is unclear.

We emphasize that these results pertain to prescribed fires, which are typically conducted only during the dry season when water levels are dropping. We believe that the effects of wildfires may be very different. Naturally ignited wildfires typically occur late in the dry season or at the beginning of the wet season and are usually more widespread and intense during periods of drought (Gunderson and Snyder 1994, Slocum *et al.* 2007). This combination often results in combustion of sawgrass rhizomes and peat, and higher mortality of sawgrass and woody vegetation (Gunderson

and Snyder 1994). Anecdotal observations suggest that these patterns are very different from prescribed burns, and could result in larger, more continuous areas of burn, the formation of depressions and large areas of belowground vegetative mortality, and the release of relatively large quantities of nutrients stored in peat and belowground biomass. Wading birds are a dominant and conspicuous part of the vertebrate biomass in fire-dominated tropical and subtropical wetlands (Frederick *et al.* 2009), and there is reason to believe that many of the more dramatic effects of wildfire (depressions, nutrient release, creation of open areas) would be compatible with enhanced prey capture or production of prey for wading birds, perhaps on somewhat longer timescales than for prescribed fire. Our results show that wading birds prefer areas recently treated with prescribed fire, and may have increased capture efficiency in recently burned areas. Together, this information suggests that there may be adaptive responses by wading birds to wetland fires that are typical of an evolved relationship, and at minimum indicates that fire can be a positive and appropriate management tool for wading birds in naturally fire-prone wetlands. We believe that further work on the effects of wildfires on wading birds, nutrient and vegetative dynamics, and aquatic prey species is now a high priority in order to understand the role of fire, and the management of fire, in wetlands.

ACKNOWLEDGMENTS

Funding for this project was provided by the US Army Corps of Engineers through a grant to Peter C. Frederick. We thank the following people for help in the field, statistical guidance, and edits: B. Bolker, R. Borkhataria, S. Coates, B. Faustini, J. Fidorra, E. Fishel, L. Garner, C. Hansen, K. Kerr, W. Loftus, J. Mansuetti, E. Posthumus, M. Schlothman, T. Schrage, J. Seavey, J.C. Simon, G. Smith, C. Stiegler, N. Vitale, A. Williams, and C. Winchester. We thank M. Ward and M. Juntunen with Florida Fish and Wildlife Conservation Commission for communicating during on-going burns and sharing burn information. We thank T.H. Parks for GIS cartography help.

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