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Factors Influencing Behavior and Success of Foraging Reddish Egrets (*Egretta rufescens*)

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Abstract.—The Reddish Egret (*Egretta rufescens*) is the rarest and least studied species of heron in North America and is a species of conservation concern throughout its range. Foraging behavior and foraging success of the Reddish Egret were studied by focusing on whether their foraging behavior or success varied with age, color morph, group size, and habitat measures. Foraging individuals ($n = 372$) were video-recorded in the Laguna Madre of Texas, USA, from March 2008–April 2010. Adult Reddish Egrets were 30–250% more successful foragers than juveniles, and groups were 32–44% more successful foragers than solitary foragers. Foraging success was similar between color morphs. The more specialized foraging behaviors of canopy feeding, wing flicking, and foot-stirring had the highest success, but were employed infrequently. Four environmental variables (wind speed, light intensity, water depth, and percent seagrass coverage) were found to influence foraging success, but accounted for only 3% of the variation in foraging behavior. Our results suggest that environmental variables have little influence on foraging behavior of Reddish Egrets in the Laguna Madre, and we suggest that characteristics of the prey have a stronger influence. An understanding of how environmental variables influence foraging behavior and success may allow us to better assess habitat quality or possibly aid in identification of highly productive foraging sites and allow for more targeted conservation actions to those habitats that promote high foraging success. *Received 12 September 2013, accepted 14 October 2013.*

Key words.—*Egretta rufescens*, foraging behavior, foraging success, group foraging, Laguna Madre, Reddish Egret.

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The Reddish Egret (*Egretta rufescens*) is restricted in its distribution, relying primarily on coastal wetland habitats. It occurs along the Gulf of Mexico, Atlantic Coast of Florida, and Pacific Coast of Mexico, as well as in the Caribbean. The Reddish Egret has an estimated 2,000 breeding pairs in the United States likely making it North America's rarest species of heron (Kushlan *et al.* 2002). The majority of Reddish Egrets breed in the United States along the Texas Gulf Coast (Lowther and Paul 2002). On average, the Laguna Madre supports 64% of the breeding population in Texas, with some years as high as 94% (Texas Colonial Waterbird Society, unpub. data). Because of the Reddish Egret's small population size and reliance on coastal wetlands, it is listed as a species of concern by the U.S. Fish and Wildlife Service and as threatened by the state of Texas (Texas Parks and Wildlife Department 2003; U.S. Fish and Wildlife Service 2008).

The Reddish Egret is described as mostly a solitary forager that defends feeding territories (Palmer 1962). The Reddish Egret feeds on small fish in relatively shallow coastal flats

and lagoons (Lowther and Paul 2002). It is the most active forager among North American herons, employing a diverse repertoire of foraging tactics (Rodgers 1983; Lowther and Paul 2002). There is evidence that species employing more active foraging techniques (e.g., chasing prey) demonstrate a lower striking efficiency than species that employ less active techniques (e.g., sit and wait) (Recher *et al.* 1983; Rodgers 1983; Kent 1987). Also, there is limited information about how foraging tactics and success vary between juveniles and adults. Reddish Egrets typically do not breed until their fourth year (Lowther and Paul 2002), and this delay could be the result of a lower foraging efficiency of juveniles making them unable to provide sufficient food for developing young. This association between deferred maturity and age-related foraging efficiency has been suggested for other waterbirds as well (Recher and Recher 1969; Bildstein 1984; MacLean 1986; Shealer and Burger 1995).

The Reddish Egret has two color morphs that may select different foraging habitats

(Green 2005). Difference in foraging habitat selection by the color morphs may justify different management strategies in different parts of their range. This is plausible because there is a north-south change in the proportion of color morphs of Reddish Egrets, with dark morphs being dominant in northern areas (e.g., upper and central Texas coast) and white morphs becoming more dominant in southern areas (B. M. Ballard, unpubl. data).

Recent interest in developing conservation strategies for the Reddish Egret has focused on increasing knowledge of important habitats used by this species (Green *et al.* 2013). However, much remains unknown about the foraging ecology of the Reddish Egret. This lack of information limits the ability to develop sound conservation strategies. For instance, understanding how environmental variables (e.g., water depth, benthic habitat) influence foraging behavior and success may allow us to better assess habitat quality or possibly aid in the identification of highly productive foraging sites (Fretwell and Lucas 1970). This would allow for more targeted conservation actions to those habitats that promote high foraging success. The protection of key foraging habitats is particularly relevant given recent energy development projects in several regions important to Reddish Egrets (Green *et al.* 2013).

Herein, we investigate the foraging ecology of the Reddish Egret with the largest sample of individuals to date, and in a region that supports over half the North American population (Texas Colonial Waterbird Society, unpubl. data). Our objectives were to investigate: 1) the relationship between the foraging behavior employed and the resulting foraging success; 2) how foraging success differed between age classes, color morphs, and solitary/group foragers; and 3) if foraging success was influenced by several environmental variables. Given the relatively active foraging behavior of the Reddish Egret, we hypothesized that foraging success would be higher for active foraging behaviors (e.g., wing-flicking, running), and in the presence of environmental variables (e.g., low water depth, minimal seagrass coverage) and attributes (e.g., adult age class, solitary foraging) conducive to active foraging.

METHODS

The study was conducted in Laguna Madre, a large (185 km long, 4-12 km wide), shallow (average depth < 1 m) lagoon along the lower Texas Coast (Fig. 1). Foraging habitat for wading birds is abundant as seagrass meadows and wind tidal flats are the two main habitat types found in the lagoon (Tunnel 2002). In particular, wind tidal flats are believed to provide the primary foraging habitat for Reddish Egrets (Lowther and Paul 2002), and they cover over 930 km² of the Laguna Madre (Quammen and Onuf 1993). The lagoon is an open-water system dominated by seagrasses, which cover about 357 km² of the basin (Quammen and Onuf 1993). Shoalgrass (*Halodule wrightii*) is the dominant species with other species including wigeongrass (*Ruppia maritima*), manatee-grass (*Cymodocea syringodium*), clovergrass (*Halophila engelmannii*), and turtlegrass (*Thalassia testudinum*) (Quammen and Onuf 1993). Seagrass habitats provide nursery and cover for a large array of baitfish that comprise the majority of the diets of wading birds.

The lower Texas Coast has a subhumid to semiarid, subtropical climate, typically with long hot summers and short mild winters (Fulbright *et al.* 1990). Average rainfall throughout the region is 68 cm. Southeastern winds predominate with north winds occurring during winter frontal passages (Tunnel 2002). Historically, the Laguna Madre routinely experienced hypersaline conditions with salinities in excess of 60 ppt (Tunnel 2002). Channelization has resulted in lower salinities by allowing for more connectivity to the Gulf of Mexico. Today, salinities in the lower Laguna Madre are usually below 40 ppt, and salinities in the upper Laguna Madre are usually around 50 ppt with freshwater inflow primarily coming from rainfall and municipal or industrial discharges (Tunnel 2002).

We divided the Laguna Madre into six zones and systematically chose one zone each survey day to video-record foraging Reddish Egrets. On each survey day, we systematically searched a zone by boat (outboard or airboat) for foraging individuals. We sampled each month from March 2008 through April 2010 and throughout the diurnal period. We video-recorded foraging individuals with a 1-40x digital camcorder for 20 min or until the bird stopped foraging. Color morph, age (hatch-year or after hatch-year), and distance to the nearest Reddish Egret and other wading bird species were recorded for each individual observed. Plumage and bill color were used to differentiate hatch-year birds from after hatch-year individuals (hereafter referred to as juvenile and adult, respectively) (Cezilly and Boy 1988). Dark morph juveniles are mostly gray with little if any distinction in color between the head/neck and the rest of the body. White morph juveniles and adults are completely white. However, juveniles of both color morphs lack plumes and bicolored bills (Lowther and Paul 2002). Birds were identified as foraging either in groups or solitary. Groups ranged from loose aggregations to tight flocks. Although there is limited information on territoriality of foraging Reddish Egrets, some evidence suggests that Great Egrets

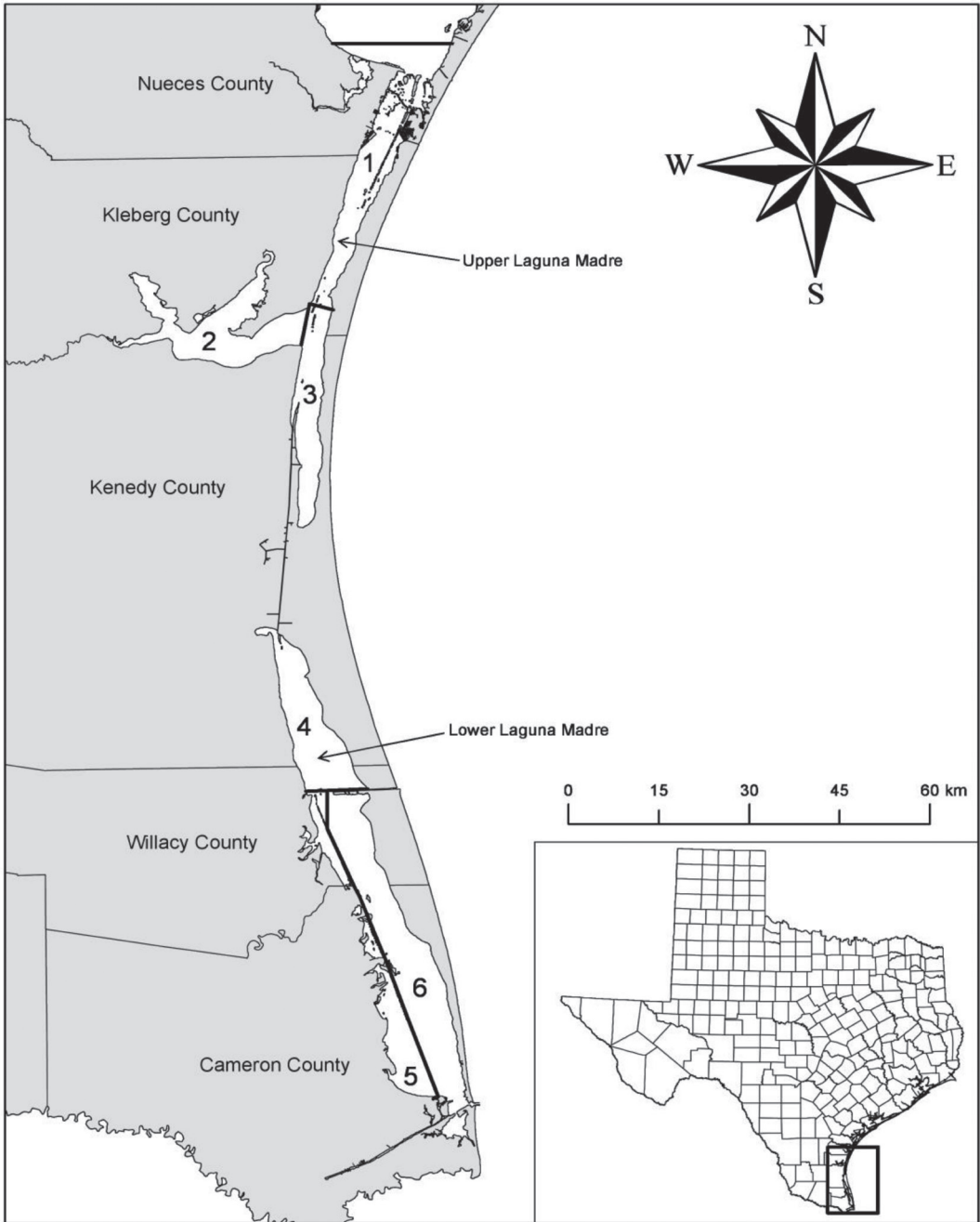


Figure 1. Study area and sampling zones for sampling foraging behavior of Reddish Egrets and associated environmental variables in the Laguna Madre, Texas, from March 2008–April 2010.

(*Ardea alba*), also considered a solitary forager, maintain a feeding territory of about 30 m unless they are foraging within a group (Wiggins 1991). Therefore, we classified a flock as \geq two Reddish Egrets foraging with $<$ 30 m of spacing between individuals during the majority of the observation period. During each observation period, average wind speed (m sec^{-1})

was measured across a 1-min time period. Also, light intensity (lux) was measured with a light meter. At the end of each observation period, we established a transect along the path of the foraging Reddish Egret and measured percent seagrass coverage and seagrass species composition with a 1- m^2 quadrat at \geq five sampling points at 25-m intervals along the transect. We

also measured water depth (cm) with a measuring stick at each sampling point.

While reviewing videos, foraging behaviors were identified and the time spent engaged in each behavior was recorded. Eight foraging behaviors, adapted from Meyerriecks (1960) and Lowther and Paul (2002), were used by Reddish Egrets in this study (Table 1). Numbers of successful and unsuccessful strikes were also recorded.

We assessed foraging success by three metrics: 1) the proportion of successful strikes (strike efficiency); 2) the number of successful strikes per minute (successful strike rate); and 3) the total number of strikes per minute (total strike rate). We used one-way ANOVAs (SAS Institute, Inc. 2008) to identify differences in foraging success independently between ages, color morphs, and between groups and solitary foragers. Multiple logistic regression (SAS Institute, Inc. 2008) was used to determine if four environmental variables (wind speed, light intensity, water depth, and percent seagrass coverage) influenced strike efficiency. Multiple linear regression (SAS Institute, Inc. 2008) was used to determine if there was a relationship between the environmental variables and successful strike rate. We tested for a relationship between successful strike rate and an interaction between water depth and percent seagrass coverage assuming the amount of seagrass should increase with increasing water depth at foraging sites. We also tested for a relationship between successful strike rate and an interaction between wind speed and light intensity because wind creates ripples on the water surface and light reflecting off those ripples creates a glistening effect possibly influencing foraging success. Candidate models were developed and ranked according to Akaike's Information Criterion (AIC_c) (Akaike 1973) to evaluate the potential extent to which the four environmental variables and the two interactions influenced strike efficiency and successful strike rate.

We used a canonical correlation analysis to model foraging behavior in relation to the four environmental variables for 351 individuals. Individuals missing any environmental data could not be used in our canonical correlation analysis and were excluded. We used one-way ANOVAs (SAS Institute, Inc. 2008) to examine differences in the proportion of time spent using the different foraging behaviors independently between ages, color morphs, and groups and individuals. Success of

the different foraging behaviors was determined by calculating strike efficiency and successful strike rate for each behavior. Any differences were considered significant at $\alpha = 0.05$.

RESULTS

We recorded foraging behavior of Reddish Egrets ($n = 372$) and sampled environmental variables at their sites of foraging during March 2008-April 2010 throughout the Laguna Madre of Texas. We recorded 4,385 min of foraging activity that captured a total of 10,408 foraging strikes, of which we were able to determine the success of 9,579 (92%) of those strikes.

Adult Reddish Egrets exhibited 30% higher strike efficiency, 2.5 times higher successful strike rate, and 60% higher total strike rate than juveniles (Table 2). No differences were found in foraging success between color morphs. On average, Reddish Egrets foraging in groups experienced a 32% higher strike efficiency and had a 44% higher successful strike rate than those foraging solitarily (Table 2). There were no differences in foraging success between juveniles foraging in groups and individually. However, adults foraged more efficiently in groups than when foraging solitarily, as group foragers experienced a 40% higher strike efficiency and a 72% higher successful strike rate than adults foraging individually (Table 2).

Environmental Variables

We detected an interaction between wind speed and light intensity on strike efficiency

Table 1. Description of eight foraging tactics used by Reddish Egrets ($n = 372$) in the Laguna Madre, Texas, from March 2008-April 2010.

Foraging Tactic	Description
Standing	Remaining stationary while foraging
Standing and probing	Keeping bill submerged in water while probing in mud
Walking	Taking less than two strides per second while foraging
Running	Taking two or more strides per second while foraging
Hovering	Hovering over the water's surface while chasing prey
Wing-flicking	Extending and retracting wings while walking or running after prey
Canopy feeding	Pulling wings over head while peering in the water
Foot-stirring	Vibrating feet in a scraping motion over the mud's surface

Table 2. Estimates (SE), test statistics, and P -values for comparisons of three measures of foraging success between ages, color morphs, and foraging classes of Reddish Egrets ($n = 372$) observed in the Laguna Madre, Texas, from March 2008-April 2010.

Characteristic	Total Strike Rate				Successful Strike Rate				Strike Efficiency				
	n	Estimate	F	df	P	Estimate	F	df	P	Estimate	F	df	P
Age													
Adult	314	2.59 (0.13)	10.00	1, 369	0.002	1.28 (0.07)	18.37	1, 369	< 0.001	0.52 (0.01)	10.37	1, 369	< 0.001
Juvenile	58	1.59 (0.29)				0.50 (0.17)				0.40 (0.04)			
Color morph													
Dark	181	2.24 (0.16)	2.82	1, 369	0.094	1.14 (0.10)	0.15	1, 369	0.698	0.52 (0.02)	1.57	1, 349	0.211
White	191	2.64 (0.17)				1.19 (0.10)				0.49 (0.02)			
Aggregation													
Groups	161	2.56 (0.18)	0.91	1, 369	0.340	1.44 (0.10)	13.53	1, 369	< 0.001	0.58 (0.02)	28.93	1, 349	< 0.001
Individuals	211	2.34 (0.16)				1.00 (0.09)				0.44 (0.02)			
Adults													
Groups	125	2.89 (0.21)	3.46	1, 311	0.064	1.72 (0.12)	22.07	1, 311	< 0.001	0.63 (0.02)	39.47	1, 296	< 0.001
Individuals	189	2.40 (0.17)				1.00 (0.09)				0.45 (0.03)			
Juveniles													
Groups	37	1.46 (0.27)	0.60	1, 56	0.440	0.51 (0.09)	0.06	1, 56	0.800	0.43 (0.05)	1.30	1, 51	0.259
Individuals	21	1.81 (0.36)				0.47 (0.12)				0.34 (0.06)			

($\chi^2 = 43.7$, $P < 0.001$). Under low light conditions, strike efficiency decreased with increasing wind speed, but as the amount of ambient light increased, strike efficiency increased with increasing wind speed. Strike efficiency was positively related to water depth ($\chi^2 = 61.4$, $P \leq 0.001$) with the odds of a strike being successful increasing by 4% for every 1 cm increase in water depth when holding the three other environmental variables constant. Strike efficiency was also positively correlated with percent seagrass coverage ($\chi^2 = 12.5$, $P \leq 0.001$) with the odds of a strike being successful increasing by 5% with every 10% increase in seagrass coverage when holding the three other environmental variables constant. We detected no interaction between water depth and percent seagrass coverage ($\chi^2 = 1.0$, $P = 0.322$) on strike efficiency. Variation in strike efficiency by foraging Reddish Egrets was best explained when all four environmental variables and the interaction between wind speed and light intensity were considered as this model accounted for 63% of all model weight for the set of a priori models (Table 3). The addition of the interaction between water depth and seagrass coverage provided less support suggesting that this interaction is not a strong predictor of strike efficiency.

We found a negative relationship ($t = -4.4$, 1; $df = 326$; $P \leq 0.001$) between successful strike rate by Reddish Egrets and percent seagrass coverage. Successful strike rate declined by 0.20 min^{-1} with every 10% increase in seagrass coverage. Wind speed, light intensity, and water depth were poor

predictors of successful strike rate as 95% confidence intervals around their beta values overlapped zero (Table 3). However, percent seagrass coverage seemed to be the best predictor out of the four environmental variables. Interactions between wind speed and light intensity, and between water depth and seagrass, were poor predictors of successful strike rate as their inclusion did not improve any of the models.

Our canonical correlation analysis created four behavior and four environmental combined canonical variables to test whether the original environmental variables could explain the use of specific foraging behaviors. The canonical variables that were produced were weighted linear combinations of the original variables created to capture as much variation in foraging behavior as possible. The first two pairs were significantly related, indicating they contain canonical correlations significantly different than zero (Table 4). Only 16% of the variance in the first canonical behavior variable is accounted for by the first canonical environmental variable, which represented the strongest relationship between the original environmental and behavior variables (Table 4). Only 5% of the variance in the second canonical behavior variable is shared by the second canonical environmental variable. The canonical redundancy analysis showed that the four canonical behavior variables explained $\leq 20\%$ of the variation in foraging behavior (Table 5). Collectively, the two significant canonical environmental variables accounted for 2.8% of the variance in foraging behaviors (Table 5).

Table 3. Parameter estimates (β values) and 95% confidence intervals for top models assessing the influence of environmental variables on the proportion of successful foraging strikes and on the successful strike rate by Reddish Egrets in the Laguna Madre, Texas, from March 2008-April 2010. Independent variables included wind speed, light intensity, water depth, and percent seagrass coverage.

Response Variable	Parameter	β	95% CI
Proportion of successful strikes	Wind	-0.118	-0.30219 – 0.06699
	Light	-0.001	-0.00120 – 0.00004
	Water Depth	0.023	-0.00751 – 0.05365
	Seagrass Coverage	-0.016	-0.02376 – -0.00878
	Wind x Light	0.001	-0.00007 – 0.00026
Successful strike rate	Light	-0.001	-0.00049 – -0.00027
	Water Depth	0.043	0.03421 – 0.05259
	Seagrass Coverage	0.003	0.00031 – 0.00599

Table 4. Results of a canonical correlation analysis examining the relationship between foraging behavior of Reddish Egrets ($n = 351$) and a set of environmental variables, both sampled from the Laguna Madre, Texas, from March 2008-April 2010.

Pair of Canonical Variables	Squared Canonical Correlation Coefficient	<i>F</i>	df	<i>P</i>
1	0.16	3.29	28, 1,227	< 0.001
2	0.05	1.71	18, 965	0.033
3	0.02	1.42	10, 684	0.167
4	0.02	1.69	4, 343	0.152

Foraging Behaviors

Overall, Reddish Egrets used foraging behaviors in relatively similar proportions between ages, color morphs, and foraging classes (Table 6). Reddish Egrets spent $\geq 48\%$ of their time walking when foraging. Standing and probing, running, hovering, canopy feeding, and wing-flicking were infrequently used, each comprising $\leq 6\%$ of the time spent foraging (Table 6). Adults appeared to spend more time in active foraging behaviors (e.g., foot-stirring and walking) than did juveniles that spent more time standing while foraging (Table 6). Foot-stirring was used three times more by adults, dark morph individuals, and those foraging in groups ($P < 0.01$). The proportion of time spent using highly active foraging behaviors (i.e., wing-flicking, hovering, and running) increased by eight times prior to and during early stages of nesting (March-May) (Fig. 2). We found that strike efficiency was relatively similar among the seven foraging behaviors, ranging from 0.42-0.65% (Table 7). The stand and probe behavior was not included in the analysis because success was difficult to determine. Although wing-flicking and canopy feeding were used relatively infrequently, they had the highest strike rate and the highest successful strike rate of all foraging behaviors. Foot-stirring had the

highest strike efficiency and also a relatively high total strike rate (Table 7). Walking, running, and hovering were the least successful foraging behaviors used by Reddish Egrets when considering all three metrics of foraging success. These three behaviors produced total strike rates and successful strike rates four to 29 times lower than canopy feeding or wing-flicking.

DISCUSSION

Adult Reddish Egrets were more successful foragers than juveniles, excelling over juveniles in all three metrics of foraging success. Similar results have been found with other heron species (Recher and Recher 1969; Rodgers 1983; Cezilly and Boy 1988; Papakostas *et al.* 2005). The lower strike efficiency and lower successful strike rate by juveniles may be the result of less developed visual-motor coordination and lack of experience such as prey identification skills or the selection of less optimal foraging sites (Draulans and Van Vesseem 1985; Cezilly and Boy 1988). Unlike Reddish Egrets in our study, juvenile wading birds often have a higher strike rate than adults (Rodgers 1983; Papakostas *et al.* 2005). However, even with a higher strike rate, juveniles typically capture prey items of smaller size than those

Table 5. Variance of foraging behaviors explained by their canonical variables and by the environmental variables for Reddish Egrets ($n = 351$) sampled in the Laguna Madre, Texas, from March 2008-June 2010.

Pair of Canonical Variables	Their Own Canonical Variables			The Opposite Canonical Variables	
	Proportion	Cumulative Proportion	Canonical <i>R</i> -square	Proportion	Cumulative Proportion
1	0.13	0.13	0.16	0.020	0.02
2	0.17	0.30	0.05	0.008	0.03
3	0.09	0.39	0.02	0.002	0.03
4	0.20	0.59	0.02	0.004	0.03

Table 6. Proportion of time spent engaged in different foraging tactics (SE) of Reddish Egrets ($n = 372$) observed in the Laguna Madre, Texas, during March 2008-April 2010.

Characteristic	Standing	Standing and Probing	Walking	Running	Hovering	Canopy Feeding	Wing-flicking	Foot-stirring
Age								
Adult	0.35 (0.010)	0.03 (0.005)	0.55 (0.010)	0.03 (0.009)	0.02 (0.003)	0.02 (0.002)	0.05 (0.004)	0.11 (0.020)
Juvenile	0.45 (0.030)	0.05 (0.010)	0.48 (0.030)	0.02 (0.030)	0.01 (0.007)	0.02 (0.005)	0.04 (0.009)	0.03 (0.040)
Color morph								
Dark	0.35 (0.020)	0.03 (0.007)	0.54 (0.020)	0.02 (0.010)	0.02 (0.004)	0.02 (0.003)	0.04 (0.005)	0.13 (0.020)
White	0.38 (0.020)	0.03 (0.008)	0.54 (0.020)	0.04 (0.010)	0.01 (0.005)	0.02 (0.003)	0.05 (0.005)	0.04 (0.020)
Foraging class								
Group	0.32 (0.020)	0.04 (0.010)	0.57 (0.020)	0.02 (0.010)	0.01 (0.007)	0.02 (0.003)	0.04 (0.006)	0.14 (0.020)
Individual	0.39 (0.020)	0.02 (0.005)	0.52 (0.020)	0.03 (0.010)	0.02 (0.004)	0.01 (0.003)	0.06 (0.004)	0.04 (0.020)

captured by adults and attain a lower food intake rate (Recher and Recher 1969; Quinney and Smith 1980; Draulans and Van Vessem 1985). Food intake rate may be more skewed for Reddish Egrets in our study compared to other studies because juveniles experienced both lower strike rate and lower strike efficiency. For species like the Reddish Egret that have a diverse repertoire of foraging behaviors, many of which are very active, there may be a steeper learning curve associated with the development of hunting skills.

Adult Reddish Egrets foraging in groups had higher strike efficiencies and higher successful strike rates than those foraging individually. Similar results have been found for species considered to have “exploiter” foraging strategies (Gawlik 2002) such as the Great Blue Heron (*Ardea herodias*) and Great Egret (Krebs 1974; Wiggins 1991; Stolen *et al.* 2012), which is much different from the searcher-type strategy of the Reddish Egret. According to Gawlik (2002), exploiters tend to remain at foraging patches even as prey density declines. Searchers, on the other hand, are adapted to find high-quality patches, exploit them, and move to find another patch when prey densities decline. Stolen *et al.* (2012) found that Snowy Egrets (*E. thula*; also considered to employ a “searcher” foraging strategy) foraged more successfully when solitary than in groups. They suggested that interference with other group members likely caused patch quality to decline for Snowy Egrets. Similarly, we did not find that juveniles realized the same increase in foraging success in groups compared to foraging solitary. This may be a result of their poorer competitive ability when in mixed flocks of adults and juveniles. Quinney and Smith (1980) found similar results for Great Blue Herons where adults attained higher foraging success when in groups, but juveniles did not.

Three hypotheses for the increased foraging success of groups have been proposed that seem applicable to Reddish Egrets. First, flocks may form at unusually productive feeding sites (Fretwell and Lucas 1970). Second, individuals in flocks may spend less time surveying for predators allowing more

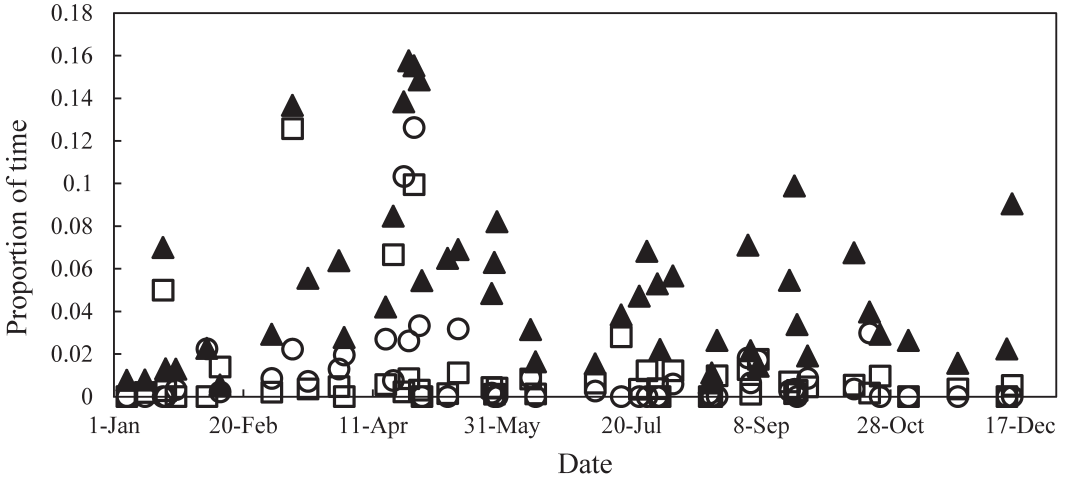


Figure 2. Average proportion of time spent running (O), hovering (□), and wing-flicking (▲) across the annual period for a sample of Reddish Egrets ($n = 372$) in the Laguna Madre, Texas.

time to be focused on foraging activities (Caraco 1979). Finally, the presence of other foraging individuals may increase the susceptibility of prey to capture (Kushlan 1978). This may be particularly relevant when prey is cryptic and mobile (Morse 1970; Hino 1998) as are the dominant prey of the Reddish Egret. However, interference competition may limit the benefits of group foraging when group size gets large (Stolen *et al.* 2012). More than one of these hypotheses may be plausible for Reddish Egrets (Powell 1985). We observed large groups (> 50 individuals) of foraging Reddish Egrets predominately during two periods of the year. The first period occurred immediately before the breeding season (January-March) and consisted mostly of adults. Foraging groups may develop at this time of year because of a decline in available foraging habitat in the

Laguna Madre (Bates 2011). The second period occurred just after the breeding season from August through October. These groups often contained a high proportion of juveniles. Juveniles may partake in group foraging to learn foraging techniques by copying behaviors of adult birds or to learn to identify productive foraging areas (Cezilly and Boy 1988). However, juveniles in our study did not appear to realize an increase in foraging success.

The more specialized foraging behaviors of canopy feeding, wing-flicking, and foot-stirring were the most successful foraging behaviors used by Reddish Egrets in the Laguna Madre and were used by adults more than juveniles. Given the greater success rates of these foraging behaviors, it is unknown why they are not employed more often. Low frequency use of specialized for-

Table 7. Average (95% CI) strike efficiency (proportion of successful strikes), successful strike rate (number of successful strikes per minute), and total strike rate (total number of strikes per minute) for seven foraging tactics used by Reddish Egrets ($n = 372$) in the Laguna Madre, Texas, during March 2008-April 2010.

Foraging Tactic	Strike Efficiency	Successful Strike Rate	Total Strike Rate
Standing	0.58 (0.56-0.60)	2.81 (2.61-3.01)	5.26 (4.98-5.54)
Walking	0.47 (0.46-0.49)	1.04 (0.86-1.22)	2.77 (2.52-3.02)
Running	0.42 (0.26-0.59)	0.92 (0.14-1.69)	2.37 (1.27-3.46)
Hovering	0.50 (0.28-0.72)	0.52 (-0.35-1.39)	1.02 (-0.21-2.24)
Canopy feeding	0.57 (0.53-0.61)	14.80 (14.18-15.42)	29.32 (28.44-30.20)
Wing-flicking	0.44 (0.41-0.47)	4.53 (4.20-4.85)	11.14 (10.68-11.60)
Foot-stirring	0.65 (0.60-0.69)	3.52 (3.09-3.96)	5.83 (5.22-6.44)

aging behaviors in wading birds has been noted by others (Willard 1977; Rodgers 1983), and may be related to local habitat conditions (Kushlan 1976). However, we found little support for the environmental variables that we measured explaining use of different foraging behaviors.

Reddish Egrets showed an increase in use of highly active foraging behaviors just prior to and during the breeding season. The breeding period is a time when energy requirements are obviously high, both from the high demands of adults and for provisioning of young. The breeding period appears to coincide with relatively high availability of foraging habitat for Reddish Egrets in the Laguna Madre due to changes in tides and winds (Bates 2011). Higher water levels typically allow prey to disperse over greater areas making them less concentrated (Kahl 1964). More active foraging behaviors may result in a higher capture rate at a time when prey may be more dispersed and when energy demands are high.

We found that the two color morphs spent similar proportions of their time among the different foraging behaviors. This is consistent with reports of similar use of foraging behaviors between color morphs of Reddish Egrets in Florida (Rodgers 1983) and Texas (Green 2005). Additionally, all three measures of foraging success were similar between the two color morphs, a finding similar to Green (2005). Although Green (2005) reported differential use of habitats between the color morphs, specifically that white morph Reddish Egrets spent more time actively foraging in deeper water than dark morph individuals, this was not the case for Reddish Egrets during the time of our study (Bates 2011).

We observed differences in use of foraging behaviors between those individuals foraging in groups and those foraging solitarily. Foot-stirring was more common among group foraging birds whereas wing-flicking was more frequently used by solitary foragers. Groups occurred primarily from August-October and from January-March. Sheepshead minnow (*Cyprinodon variegatus*), the primary prey of the Reddish Egret (Lowther

and Paul 2002), will burrow into the mud as a form of behavioral thermoregulation when temperatures drop (Bennett and Beitinger 1997). Groups of Reddish Egrets foraging during winter may use foot-stirring if prey have burrowed into the substrate. When foraging groups are formed in areas with high prey density (Kushlan 1976; Hafner *et al.* 1993), there may be limited need to use more active foraging behaviors because other birds foraging in close proximity likely disturb prey and make them more vulnerable to predation (Morse 1970; Hino 1998).

We found that little variation in foraging behavior was explained by the four environmental variables measured. This is consistent with Rodgers (1983) who found little support for environmental variables explaining variation in foraging behaviors employed by a variety of wading bird species. It appears that density and behavior of prey may be more important predictors of foraging behavior than environmental variables. For example, Kasner and Dixon (2003) observed Great Egrets and Snowy Egrets foraging aerially on shad (*Dorosoma* sp.) being forced to the surface by white bass. Additionally, group foraging by Little Egrets (*E. garzetta*) was more common in early mornings when mosquito fish were concentrated due to temporally patterned hypoxic conditions in wetlands (Hafner *et al.* 1993). These examples demonstrate the ability of wading birds to adjust their foraging behaviors in relation to prey type and behavior. This also may explain the increase in use of active foraging behaviors when foraging habitat availability increased and prey density and behavior likely changed.

Environmental variables appeared to have an influence on foraging success. Under low light conditions, strike efficiency decreased with increasing wind speed, but as the amount of ambient light increased, strike efficiency increased with increasing wind speed. Rodgers (1983) found that wind increased wave action, which decreased foraging success of herons. Also, the combination of bright ambient light and windy conditions could possibly result in a decrease in the ability of prey to detect predators resulting in an increase in their vulnerability. Sea-

grass coverage also had somewhat varying effects on foraging success. Although strike efficiency increased with increasing seagrass cover, we found that successful strike rate decreased with increasing seagrass coverage. Thus, fewer strikes were made as seagrass cover increased, probably because of a decrease in encounter rate. Consequently, it appeared that the reduction in successful strike rate outweighs any benefits from the increase in strike efficiency. This seems plausible given that the Reddish Egret focuses its foraging in areas with little to no seagrass coverage (Bates 2011).

Our findings add support to previous work that found environmental variables to poorly predict the use of foraging behaviors by Reddish Egrets and other wading birds (Rodgers 1983; Stolen *et al.* 2012). Future studies should examine the effect of the ecology and behavior of prey species on Reddish Egret foraging behaviors. Also, investigations of how environmental variables (e.g., water temperature and dissolved oxygen) affect the availability and behavior of prey and the resulting effects on Reddish Egret foraging behavior would provide more insight to the predator-prey dynamics in this system. This would be of particular interest given the large fluctuations in foraging habitat availability in the Laguna Madre (Bates 2011) and its influence on the partial migration strategy employed by Reddish Egrets in this lagoon (B. M. Ballard, unpubl. data). Examining the relationships between habitat, environmental variables, and prey should yield a better understanding of Reddish Egret foraging behavior. Also, even though the Reddish Egret is considered a solitary forager, we observed relatively large foraging groups that achieved relatively high foraging success. Further studies should examine the mechanisms by which these foraging flocks form and examine the benefits gained by feeding in these flocks, particularly for juveniles.

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