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Comparisons of Reddish Egret (*Egretta rufescens*) Diet During the Breeding Season Across its Geographic Range

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Abstract.—Although the prey of Reddish Egrets (*Egretta rufescens*) generally consists of shallow-water, euryhaline fish species, rangewide differences in breeding season diet have not been examined. Furthermore, the relative proportions of the two Reddish Egret color morphs vary from east to west across the species' range. Color morph may influence foraging efficiency, but variations in prey across the species' range and between morphs is undocumented. By examining boluses from Reddish Egret ($n = 109$) nestlings, prey species proportions were compared between morphs, among regions and among colonies within Texas. Between regions, prey species and proportion of species differed widely; however, fish species with similar life histories were selected across the Reddish Egret's range (Bahamas: 100% sheepshead minnow (*Cyprinodon variegatus*); Texas: 85% sheepshead minnow; Baja California Sur: 49% American shadow goby (*Quiatula y-cauda*); Yucatán: 64% Yucatán pupfish (*C. artifrons*)). Within the Laguna Madre in Texas, significant differences in prey species were not detected between morphs ($F_{(1,61)} = 1.36, P = 0.224$); however, prey mass by species differed between colonies ($F_{(1,60)} = 2.68, P = 0.010$). While our results only pertain to Reddish Egret diet during the breeding season, this study increases our understanding of Reddish Egret ecology and provides initial diet information across the species' range. Received 9 September 2013, accepted 12 November 2013.

Key words.—Bahamas, Baja California Sur, color polymorphism, Cyprinodontidae, *Egretta rufescens*, Reddish Egret, Texas, Yucatán.

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The use of shallow tidal flats and estuaries by Reddish Egrets (*Egretta rufescens*) as foraging habitat remains relatively consistent across the range of the species (Lowther and Paul 2002). The Reddish Egret has the most varied and active foraging techniques of any North American heron, using most of the foraging methods exhibited by herons (Meyerriecks 1960; Kushlan 1978; Rodgers 1983; Green 2005). Foraging techniques include stand and wait, wading, peering, wing-flicking, canopy feeding, and, most commonly, disturb and chase (Meyerriecks 1960; Rodgers 1983). Reddish Egrets typically forage in less than 30 cm of water (Lowther and Paul 2002), but they may use different foraging strategies depending on wa-

ter depth, other habitat conditions (Rodgers 1983; Green 2005), and potentially prey. The prey of Reddish Egrets is composed of shallow-water, schooling, euryhaline fish species (McMurry 1971; Simersky 1971; Paul 1991; Ramo and Busto 1993); however, rangewide differences in breeding season diet have not been examined.

Clinal variation of plumage morphs in the dimorphic Reddish Egret occurs along an east-west gradient with western populations (e.g., Baja California Sur) consisting entirely of dark morph individuals and easternmost populations (e.g., Bahamas) consisting of mostly (~88%) white morph individuals (Bolen and Cottam 1975; Howell and Pyle 1997;

Green *et al.* 2011; Hill *et al.* 2012). In Texas, within the geographic middle of their range, the ratio of dark:white morph individuals is nearly 1:1, with dark morphs slightly more common (Holderby *et al.* 2012). Over this longitudinal gradient, differences occur in weather patterns, water conditions, foraging habitat, nesting habitat, and prey species (Lowther and Paul 2002).

Dark-white polymorphism potentially affects prey selection in that plumage color can affect the foraging efficiency of Reddish Egrets in different habitats or on certain prey species (Mock 1980; Green 2005; Green and Leberg 2005). Documentation of dark morphs spending more time foraging in shallower waters than white morphs (Green 2005) supports the hypothesis that foraging strategies are related to crypsis to prey in Reddish Egrets. There is some evidence that foraging differences also occur between color morphs in Pacific Reef Herons (*E. sacra*). Rohwer (1990) observed a

preference for deeper, turbid water by white morphs and selection of less turbid, shallower waters by dark morphs.

The objectives of this study were to: 1) investigate rangewide prey species composition of Reddish Egrets during the breeding season; and 2) examine the influence of color morphs and colony location on prey composition of Reddish Egrets in Texas.

METHODS

We collected chick regurgitate (hereafter bolus) from Reddish Egret nestlings in Texas, Baja California Sur, Yucatán and the Bahamas. Four colonies of Reddish Egrets within the Laguna Madre hyper-saline lagoon between Corpus Christi and Port Isabel, Texas, USA were sampled opportunistically during banding excursions (May-June 2007; Fig. 1). Nestlings also were sampled during banding excursions on Great Inagua, Bahamas (April 2012; details in Green *et al.* 2011); at Laguna La Carbonera (La Marca colony), Yucatán, Mexico (19-20 April 2012 at 21° 11' 53.46" N, 89° 56' 47.52" W); and at Isla Piedras, Baja California Sur, Mexico (collected on 22 June 2012 at 27° 42' 4.68" N, 114° 9' 13.68" W).

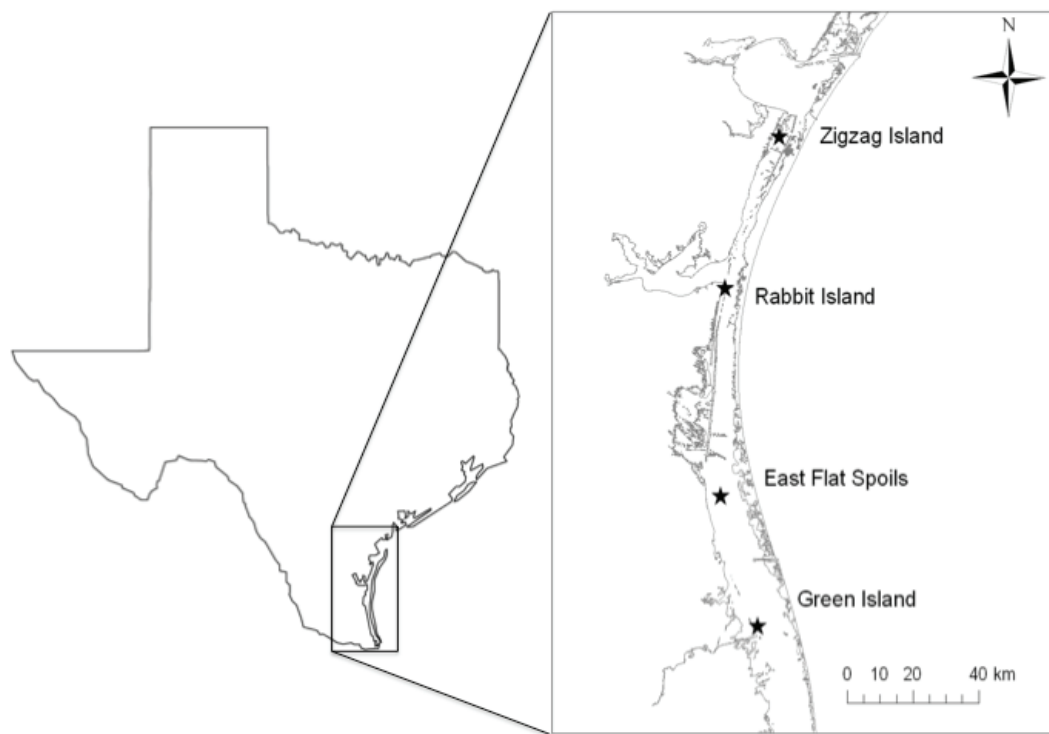


Figure 1. Major Reddish Egret colonies in the Laguna Madre, Texas. Stars signify colonies where prey samples were collected from nestling boluses. Samples from Zigzag Island and Rabbit Island were classified as Upper Laguna Madre and samples from East Flat Spoils and Green Island were classified as Lower Laguna Madre.

In Baja California Sur and Yucatán, all nestlings were dark morphs, whereas in the Bahamas all nestlings were white morphs. Typically, when chicks are approached or handled for banding, some will regurgitate all or a portion of their last meal. All boluses collected at an individual nest were placed in a bag and considered one sample. After identifying all prey, we calculated the frequency of each prey species at each site.

In Texas, we collected samples from dark and white morph nestlings. The color morph of the nestlings, colony location, date, prey species, and weight per species were recorded for each sample. We assumed color morph of nestlings was representative of color morph of parents based on 157 nest observations (Rabbit Island: $n = 79$, 53 dark morph and 26 white morph nests; Zigzag Island: $n = 78$, 38 dark morph and 40 white morph nests) during a concurrent study of nesting ecology of Reddish Egrets in Texas; behavioral studies at the colonies indicated all nests had same morph nestlings attended by same morph adults (Holderby 2009). Although we documented six mixed-morph nests in this concurrent study, we did not include regurgitate from mixed-morph nestlings. We calculated: 1) the proportion represented by each prey species; and 2) the percentage of total mass that each prey species represented in the samples. Samples were compared among colony sites and between color morphs using a MANOVA (Zar 1996) on the proportion of occurrence of prey items per sample. A separate MANOVA (Zar 1996) was conducted to compare the proportion of biomass of each prey species between colony sites and color morph. Proportional data was Arcsine transformed prior to statistical analyses (Zar 1996). We classified the Texas colonies as either Upper Laguna Madre (Zigzag Island and Rabbit Island) or Lower Laguna Madre (East Flat Spoils and Green Island) to examine potential prey differences within the hyper-saline lagoon. All statistical analyses were conducted using program R (R Core Development Team 2008).

RESULTS

Regardless of geographic location, most samples (> 75%) were dominated by one or two species of fish. Texas and Bahamas sam-

ples contained mostly sheepshead minnow (*Cyprinodon variegatus*), Baja California Sur samples contained mostly American shadow goby (*Quietula y-cauda*) and sargassum blenny (*Exerpes asper*) (Table 1), while Yucatán samples contained mostly Yucatán pupfish (*Cyprinodon artifrons*) (Table 2). In the Bahamas, sheepshead minnow was the sole component of Reddish Egret regurgitate, although our sample size was low ($n = 6$). Regurgitate samples from Texas contained a larger diversity of prey items, but sheepshead minnow (84%) and tidewater silverside (*Menidia peninsulae*, 7%) dominated, comprising 91% of the diet ($n = 67$). Though no species and only one family were shared between Texas and Baja California Sur, Baja California Sur was similarly dominated by three species, representing > 90% of regurgitate: the American shadow goby (48.8%), sargassum blenny (27.3%), and California killifish (*Fundulus parvipinnis*, 15.6%) ($n = 22$). Other prey species present in Reddish Egret samples typically comprised less than 3% of the total diet. Species composition of Yucatán samples differed from other populations however; like Texas and Bahamas, prey species from the family Cyprinodontidae represented ~81% of species consumed by Reddish Egrets.

Within the Laguna Madre of Texas, prey composition did not differ between morphs ($F_{1,61} = 1.36$, $P = 0.224$; Table 3). Also, there was no significant interaction between morph and colony site ($F_{1,61} = 0.56$, $P = 0.839$). Diet composition as a whole did not significantly vary among colony sites ($F_{1,61} = 1.46$, $P = 0.182$; Table 4; Fig. 2). There were significant differences

Table 1. Percentage of prey items consumed, as identified in Reddish Egret chick boluses from Isla Piedras, Baja California Sur, Mexico ($n = 22$).

Family	Species	Frequency (%)
Fundulidae	<i>Fundulus parvipinnis</i>	15.6
Syngnathidae	<i>Syngnathus auliscos</i>	0.3
Labrisomidae	<i>Exerpes asper</i>	27.3
Labrisomidae	<i>Paraclinus integripinnis</i>	0.7
Blenniidae	<i>Hyposoblennius gentilis</i>	0.2
Gobiidae	<i>Quietula y-cauda</i>	48.8
Paralichthyidae	<i>Paralichthys californicus</i>	0.8
Pleuronectidae	<i>Hypsopsetta guttulata</i>	6.3

Table 2. Percentage of prey items consumed and percentage of biomass consumed, as identified in Reddish Egret chick boluses from La Marca, Yucatán, Mexico ($n = 14$).

Family	Species	Frequency	Mass
Engraulidae	Anchovy spp.	1.2	0.5
Poeciliidae	<i>Belonesox belizanus</i>	1.2	2.7
Cyprinodontidae	<i>Cyprinodon artifrons</i>	64.0	41.8
Gerreidae	<i>Eucinostomus harengulus</i>	0.2	1.6
Gerreidae	<i>Eucinostomus</i> spp.	1.2	0.7
Cyprinodontidae	<i>Floridichthys polyommus</i>	5.1	26.4
Fundulidae	<i>Fundulus grandissimus</i>	0.6	4.2
Fundulidae	<i>Fundulus persimilis</i>	1.2	7.6
Poeciliidae	<i>Gambusia yucatana</i>	4.3	0.6
Cyprinodontidae	<i>Garmanella pulchra</i>	12.1	3.0
Atherinopsidae	<i>Menidia colei</i>	2.6	1.2
Cichlidae	<i>Cichlasoma urophthalmus</i>	0.2	0.3
Poeciliidae	<i>Poecilia velifera</i>	1.2	3.8
Poeciliidae	<i>Poecilia</i> spp.	4.0	4.8
Belonidae	<i>Strongylura notata</i>	0.2	0.7
	Unidentified	0.7	0.1

in diet composition by weight of species components among islands ($F_{1,60} = 2.68$, $P = 0.010$) for tidewater silverside ($F_{1,60} = 4.72$, $P = 0.034$), pinfish (*Lagodon rhomboids*) ($F_{1,60} = 4.14$, $P = 0.046$), mullet (*Mugil* sp.) ($F_{1,60} = 4.14$, $P = 0.046$), pink shrimp (*Penaeus duorarum*) ($F_{1,60} = 5.71$, $P = 0.020$) and spot (*Leiostomus xanthurus*) ($F_{1,60} = 5.40$, $P = 0.023$). Tidewater silverside, pinfish, spot and pink shrimp were all a larger proportion of the total mass of Reddish Egret chick diet in the Lower Laguna Madre, whereas mullet were a larger proportion of total mass in the Upper Laguna Madre.

DISCUSSION

As seen in previous studies, sheepshead minnow represented the primary prey in the diet of Reddish Egret chicks in Texas (McMurray 1971; Simersky 1971; Paul 1991). The sheepshead minnow's occurrence in shallow estuaries makes it an ideal prey species for Reddish Egrets (Johnson 1980). In the Laguna Madre, sheepshead minnow can be very abundant where the bottom is at least partially sandy, emergent vegetation is lacking and the water is calm (Johnson 1980). During peak spawning from April

Table 3. Comparison between color morphs of Reddish Egrets in the percentage of prey items consumed and percentage of biomass consumed, as identified in chick boluses collected in the Laguna Madre, Texas (Dark morph: $n = 37$; White morph: $n = 29$).

Family	Species	Dark Morph		White Morph	
		% Prey	% Mass	% Prey	% Mass
Clupeidae	<i>Alosa chrysochloris</i>	0.4	1.3	0.3	1.3
Mugilidae	<i>Mugil</i> spp.	1.3	4.4	1.4	4.1
Atherinopsidae	<i>Menidia peninsulae</i>	7.4	7.9	6.2	11.3
Belonidae	<i>Strongylura marina</i>	0.1	0.1	0.2	0.2
Fundulidae	<i>Fundulus similis</i>	1.5	8.2	0.6	0.4
Cyprinodontidae	<i>Cyprinodon variegatus</i>	84.8	60.5	83.6	59.1
Sparidae	<i>Lagodon rhomboids</i>	0.9	6.0	3.8	13.9
Sciaenidae	<i>Leiostomus xanthurus</i>	1.1	4.2	1.3	7.3
Sciaenidae	<i>Umbrina coroides</i>	1.4	5.6	0.1	0.1
Penaeidae	<i>Penaeus duorarum</i>	0.4	0.3	2.4	2.1
	Unidentified	0.7	1.5	0.1	0.2

Table 4. Comparison between sites within the Laguna Madre in the percentage of prey items consumed and percentage of biomass consumed, as identified in Reddish Egret boluses collected in the Laguna Madre, Texas (Lower Laguna: $n = 24$, Upper Laguna: $n = 43$). * denotes significant differences ($P \leq 0.05$) between Upper and Lower Laguna Madre in prey items or biomass consumed.

Family	Species	Lower Laguna		Upper Laguna	
		% Prey	% Mass	% Prey	% Mass
Clupeidae	<i>Alosa chrysochloris</i>	0.2	0.6	0.4	1.7
Mugilidae	<i>Mugil</i> spp.	0.0	0.0*	2.4	6.9
Atherinopsidae	<i>Menidia peninsulae</i>	13.0	21.5*	1.4	1.1
Belonidae	<i>Strongylura marina</i>	0.2	0.6	0.2	0.1
Fundulidae	<i>Fundulus similis</i>	0.5	0.2	1.5	7.3
Cyprinodontidae	<i>Cyprinodon variegatus</i>	74.3	39.6	92.0	72.2
Sparidae	<i>Lagodon rhomboids</i>	5.0	19.2*	0.3	3.1
Sciaenidae	<i>Leiostomus xanthurus</i>	3.0	13.5*	0.2	1.7
Sciaenidae	<i>Umbrina coroides</i>	0.4	1.9	1.0	3.6
Penaeidae	<i>Penaeus duorarum</i>	3.2*	2.8*	0.0	0.0
	Unidentified	0.2	0.1	0.6	2.3

through July (Gunter 1950), large numbers of sheepshead minnows may accumulate in the shallower waters of the Laguna Madre (Allen 1942); these dates roughly correspond with Reddish Egret hatch dates within the Laguna Madre (Holderby *et al.*

2012). Gunter (1945) found that in very shallow water sheepshead minnow is one of the predominant species, along with tide-water silverside. Sheepshead minnow also has a high tolerance to temperature and salinity variations (Kilby 1955; Bennett and

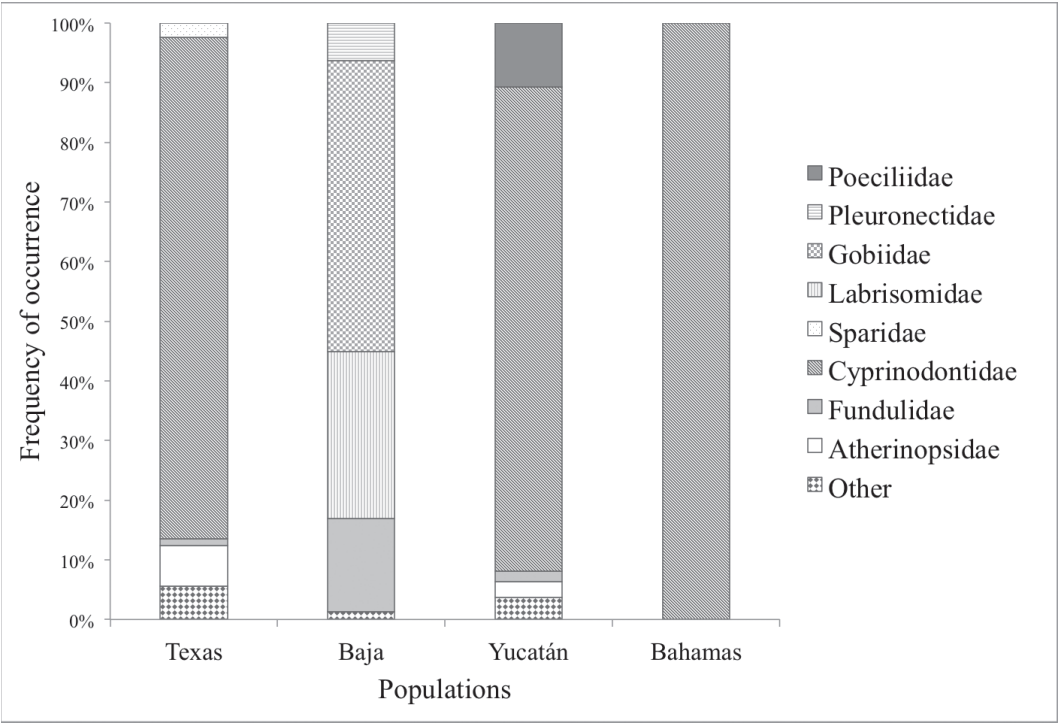


Figure 2. Comparison of frequency of occurrence (%) of major aquatic prey species in chick boluses between Reddish Egret populations in Laguna Madre, Texas ($n = 67$); Isla Piedras, Baja California Sur, Mexico ($n = 22$); La Marca, Yucatán, Mexico ($n = 14$); and Lake Rosa, Great Inagua, Bahamas ($n = 6$).

Beitinger 1997). The natural history of the sheepshead minnow, a species that lives and reproduces in large numbers in these calm, coastal flats, presumably explains why this species consistently represents over 80% of the Reddish Egret diet in Texas during the breeding season.

In the limited samples from the Bahamas, the only fish species found in regurgitate samples was sheepshead minnow. This monotypic sampling of sheepshead minnow is likely due to the large hyper-saline lake on Great Inagua that concentrates fish, oxygen and salt. Sheepshead minnow may be one of the few fish that can tolerate these environmental extremes (Kilby 1955; Bennett and Beitinger 1997). Presumably, in other areas of the Caribbean and Florida, additional species are also a component of the Reddish Egret diet. In Florida, sheepshead minnow represented > 53% of species identified from chick regurgitate with sailfin molly (*Poecilia latipinna*) and goldspotted killifish (*Floridichthys carpio*) also occurring (Paul 1991). Future studies should include more sampling of diet from Florida, Great Inagua and other sites in the Caribbean.

The Reddish Egret's diet in Yucatán was composed of two permanent resident fish, Yucatán pupfish and ocellated killifish (*Floridichthys polyommus*), and one seasonal species, Yucatán flagfish (*Garmanella pulchra*), all estuarine species (Gallardo-Torres *et al.* 2012). Of these, Yucatán pupfish and ocellated killifish are abundant species along the Yucatán coast (Vega-Cendejas and Hernández de Santillana 2004; Gallardo-Torres *et al.* 2012). The Yucatán pupfish, similar to the sheepshead minnow, can tolerate extreme salinity (Vega-Cendejas and Hernández de Santillana 2004). Our results differed from an earlier study of Reddish Egret diet in the Yucatán in species composition but not proportion (Ramo and Busto 1993). Ramo and Busto (1993) identified *Cyprinodon variegatus* (~69%) and *Floridichthys carpio* (~7%) in Reddish Egret chick boluses at Sian Ka'an Biosphere Preserve, whereas we report *C. artifrons* (~64%) and *F. polyommus* (~5%) and did not document either *C. variegatus* or *F. carpio*. For the Cyprinodontidae family, we suggest that the species documented in both

studies were *C. artifrons* (Yucatán pupfish) and *F. polyommus* (ocellated killifish); both species were originally classified as subspecies, *C. variegatus artifrons* and *F. carpio polyommus*, respectively (Hubbs 1936).

In Baja California Sur, sheepshead minnow are absent and almost 50% of the Reddish Egret's breeding season diet is composed of American shadow goby. Though the ecology of the American shadow goby is poorly documented, the species can be abundant in shallow mud flats of lagoons and river deltas and reproduction is assumed to occur in estuarine waters peaking from April to June (Eschmeyer *et al.* 1983). The possible similarities in life histories between *Gobiomorus* and *Cyprinodon* suggest the species are ecological equivalents, and *Gobiomorus* represents a suitable alternative prey species for Reddish Egrets during the breeding season on the Pacific Coast (Miller and Lea 1972). The second most common species collected in chick boluses, the sargassum blenny, is a benthic species and is most commonly found in reefs and rocky substrate. The potential habitat differences between the two most frequent prey items suggests Reddish Egrets may forage in a wider range of coastal habitats than seen in Texas and the Bahamas. Little is known about the foraging ecology of Reddish Egrets in western Mexico; future studies are warranted to examine habitat use by Reddish Egrets in the western portion of its range. Other fish of the shallow estuarine waters (e.g., California killifish) comprised a smaller portion of the diet and are potentially taken opportunistically relative to local abundance within foraging habitats.

Diet differences between morphs in Texas were small and insignificant. While chick morph was used to assume adult morph, on rare occasions this may not be correct. Our assumption is based on a concurrent behavioral study (Holderby 2009) that found all focal nests to be monotypic and mixed-fledgling nests to be rare. Pinfish and pink shrimp were found in larger numbers in white morphs compared to dark morphs; however, low sample size prevents any strong inferences. Both pinfish (Muncy 1984) and

pink shrimp are species that tend to be deeper in the water column; this may reflect preferences in foraging depth (Green 2005). However, neither prey species was common in boluses, illustrating that potential niche separation in diet between color morphs is presumably negligible, or that differences in fish composition do not vary greatly within the range of Reddish Egret foraging depths.

Differences in diet between islands in Texas were more apparent. Pink shrimp was the only food item that significantly differed in frequency of occurrence between the upper and lower Laguna Madre whereas mullet, tidewater silverside, pinfish, spot and pink shrimp all differed by mass between island groups; these variations in prey composition and mass presumably reflects differences in aquatic habitat in proximity to the nesting colonies. The differences in prey composition and mass may be related to differences in water depth, salinity, disturbance, and aquatic vegetation between the two colony sites and could have implications for varying nesting success at colonies across the Laguna Madre (Holderby *et al.* 2012). Foraging habitat differences between these colonies should be studied in greater detail.

Large differences in Reddish Egret diet during the breeding season occurred across the species' range. While no prey species are shared between the Baja California Sur and Gulf of Mexico populations, one to three species appear to represent the majority of prey items fed to chicks in each region. Reddish Egrets do not appear to be pre-adapted to specific prey species, but rather to shallow water habitat types that attract similar species. It is important to note that our results only pertain to Reddish Egret diet during the breeding season. The proximity of available foraging habitat in relation to breeding sites and the need for prey of a suitable size for chicks limits our inferences about Reddish Egret diet outside the breeding season. It is plausible that Reddish Egrets may shift the prey composition and/or size of their diet outside the breeding season. Potential trophic shifts and variations in prey size during migration and over-wintering periods are unknown and warrant future investigation.

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