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Authors: Koczur, Lianne M., Kent, Gina M., Ballard, Bart M., Meyer, Kenneth D., and Green, M. Clay

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Space Use and Movements of Adult Reddish Egrets (*Egretta rufescens*) During Winter

LIANNE M. KOCZUR^{1*}, GINA M. KENT², BART M. BALLARD¹, KENNETH D. MEYER² AND M. CLAY GREEN³

¹Caesar Kleberg Wildlife Research Institute, MSC 218, 700 University Boulevard, Texas A&M University-Kingsville, Kingsville, Texas, 78363, USA

²Avian Research and Conservation Institute, 411 NE 7th Street, Gainesville, Florida, 32601, USA

³Department of Biology, 601 University Drive, Texas State University, San Marcos, Texas, 78666, USA

*Corresponding author; E-mail: LianneKoczur@gmail.com

Abstract.—The Reddish Egret (*Egretta rufescens*) is listed as a priority species for conservation throughout much of its range because of a relatively small global population size and restriction to coastal habitats. Much of the previous research on the Reddish Egret has focused on the breeding season; subsequently, little is known about the winter ecology of the species. Satellite transmitters were attached to adult Reddish Egrets breeding in the USA in Texas ($n = 30$) and Florida ($n = 5$) and daily movements were tracked during the winters of 2010-2016. Reddish Egrets that were marked during the breeding season in Texas, USA, wintered at sites in Texas, Mexico, and El Salvador, and those marked in Florida, USA, remained resident. Habitat types used for foraging and roosting were similar in Texas; 48% of roost locations and 63% of foraging locations occurred on unvegetated tidal flats. In Florida, Reddish Egrets used different habitats for roosting compared to foraging. All Reddish Egrets exhibited a high degree of fidelity to wintering sites across years; 72% of individuals had an average overlap of $\geq 63\%$ for roosting areas across successive winters, and 78% had an average of $\geq 65\%$ for foraging areas. Average home range sizes varied considerably among locations and sexes and ranged from 39 ha (95% CI = 7-224; males in Florida) to 11,849 ha (95% CI = 4,946-28,282; females at western Gulf Coast sites). This study provides new information on the winter ecology of Reddish Egrets that will aid in directing conservation and management efforts for the species. Received 10 July 2017, accepted 26 August 2017.

Key words.—*Egretta rufescens*, El Salvador, Florida, habitat use, Mexico, nonbreeding, Reddish Egret, Texas, winter.

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Much of the research on waterbird ecology emphasizes the importance of breeding sites and reproductive success (Kelly *et al.* 2008; Auclair *et al.* 2015; Baker and Dieter 2015). Studies conducted during the breeding season can often be comparatively simple, as the focal animal is restricted to the nesting area. More logistically challenging is examining the wintering ecology of a species, particularly when they are migratory. Understanding the habitat requirements and conditions at a species' winter site is critical in our knowledge of the complete annual cycle. Furthermore, recent research has revealed that performance in one portion of the annual cycle (e.g., nonbreeding) can influence performance during another (breeding) (Sedinger and Alisauskas 2014).

The distribution of the Reddish Egret (*Egretta rufescens*) is restricted to shallow, coastal wetlands along the Gulf Coast of the United States and Mexico, the Sea of Cortez and Pacific Coasts of Mexico, and throughout much of the Caribbean (Lowther and Paul 2002). Habitat requirements during winter include those for foraging and roosting. There are multiple factors that may influence roost site selection and roosting behavior in waterbirds, including the specific season, time of day, weather, tide level, degree of coloniality, distance from roosting to foraging sites, foraging strategies, predator avoidance, and level of human disturbance (Luís *et al.* 2001). Similar factors influence foraging habitat availability and use by waterbirds. Foraging habitat and behavior of

nonbreeding Reddish Egrets have been examined in Texas, USA (Bates and Ballard 2014; Bates *et al.* 2016). Whereas water depth requirements should be the same across the species' range, the benthic habitat that is used may vary across geographic locations. Furthermore, there may be individual variation in habitat use. Little is known about the roosting habitat requirements of Reddish Egrets. Although roosting habitat is considered to be indistinguishable from foraging habitat (Wilson *et al.* 2014), there have been no comparative studies on the habitat of foraging and roosting areas.

It is well known that bird populations use the same roosting and foraging sites for many years (Rehfisch *et al.* 2003; Conklin and Colwell 2007), yet site fidelity at the individual level has been more challenging to ascertain, as researchers have relied on banding and resighting, or radio telemetry. Thus, if individuals were not resighted or detected, or did not return to the same location, it was unknown if they had died prior to returning, had returned but were simply not observed or detected, or were not faithful to previously used sites. The recent use of satellite transmitters equipped with GPS capabilities has made it possible to more accurately determine individual site fidelity (García-Ripollés *et al.* 2010; Clark *et al.* 2016). Fidelity to winter sites can be an important metric, because identification of sites that are used faithfully by a significant portion of a population should be a priority for habitat conservation (Wilson *et al.* 1991; Warkentin and Hernández 1996).

The Reddish Egret is one of the least studied heron species in North America. The species is listed as near threatened by the International Union for Conservation of Nature (BirdLife International 2016), State listed as threatened in Texas (Texas Natural Diversity Database 2017), State listed as threatened in Florida (Florida Fish and Wildlife Conservation Commission 2017), and federally listed as a species of special concern in Mexico (Secretaría de Medio Ambiente y Recursos Naturales 2010). Reddish Egrets that were banded during the breeding season in Texas, USA, have been

resighted in Oaxaca, Mexico, and El Salvador (Lowther and Paul 2002); however, the extent of migration and location of wintering areas by migratory Reddish Egrets are relatively unknown. Examining the wintering ecology of the Reddish Egret will provide important information on this species, as previous research of Reddish Egret ecology has focused on reproductive success and foraging behavior (Holderby *et al.* 2012; Bates and Ballard 2014). The objectives of this study were to determine: (1) fidelity to wintering areas; (2) habitat characteristics of roosting and foraging locations; and (3) differences in habitat use across various portions of the species' range.

METHODS

Study Area

Gulf Coast. The Laguna Madre of Texas, USA, is a 365,800-ha hypersaline lagoon, averaging ~1 m in depth (Fig. 1A). It contains extensive areas of seagrass (*Halodule wrightii*, *Ruppia maritima*, *Syringodium filiforme*, *Thalassia testudinum*) and wind tidal flats (Tunnell and Judd 2002). Laguna Madre is bordered on the east side by a barrier island, including the Padre Island National Seashore and South Padre Island (Tunnell and Judd 2002). On the mainland side, undeveloped rangeland dominates the landscape, but other land use includes agricultural fields, wind farms, and suburban developments. The Rio Grande River Delta is located between Laguna Madre, Texas, USA, and Laguna Madre de Tamaulipas, Tamaulipas, Mexico, and is composed of coastal wetlands, distributary channels from the Rio Grande, oxbow and playa lakes, and wind tidal flats (Tunnell and Judd 2002). The Laguna Madre of Tamaulipas is 570,000 ha (Fig. 1A), is a Natural Protected Area and supports breeding and wintering Reddish Egrets.

The Laguna de Términos is a 750,032-ha lagoon in Campeche, Mexico (Fig. 1B). It was designated a nature reserve in 1994 and is listed as an Important Bird Area (Vidal *et al.* 2009) and as a wetland of international importance by the Ramsar Convention. Although the reserve is largely protected, the conversion of forest to cattle (*Bos taurus*) ranches has increased along its borders. It is also threatened with degradation due to cutting of mangroves (*Rhizophora mangle*, *Avicennia germinans*), road construction, and other human-related causes (Bach *et al.* 2005).

Hagens Cove is located on the Gulf Coast of Florida, USA (Fig. 2A). It is nearly 54 ha of hardpan, shallow, tidal cove with a variety of seagrasses. The site is especially important for Reddish Egrets in the fall and winter months, where as many as 22 individuals have been seen foraging at one time. Sanibel Island and Pine Island are

located on the central Gulf Coast of Florida (Fig. 2B). The area has a series of tidal impoundments where Reddish Egrets gather at the outflow culverts at low tide as fish concentrate over the hardpan sand fan created by the concentrated water currents. Boca Grande Key is a 74-ha island that is in the Florida Keys (Fig. 2C). An extensive tidal lagoon runs north to south on the west side of the key creating ideal forage for many species of birds that may nest in the mangroves on the eastern side or that use the key during the non-breeding season. Cudjoe Key, also part of the Florida Keys, is a 1,450-ha island located ~35 km east of Boca Grande Key (Fig. 2C). Much of Cudjoe Key has shallow salt water ponds in remote areas.

Pacific Coast. Laguna del Mar Muerto is on the southern coast of the Tehuantepec Isthmus in Oaxaca and Chiapas, Mexico, and encompasses 70,000 ha (Fig. 3A). A survey of breeding colonies along the western coast of Mexico found that Laguna del Mar Muerto supported the largest breeding colony of Reddish Egrets on the Pacific Coast, with ~258 pairs (Palacios *et al.* 2010). The Rio Verde is a 342-km-long river located in Oaxaca, Mexico (Fig. 3A). The Rio Verde basin covers 2,586 km² and spans ~64 km from east to west between two mountain ranges. The habitat was described by Binford (1989) as arid tropical scrub, tropical deciduous forest, and arid pine-oak (*Pinus* spp., *Quercus* spp.) forest. There is little information available on habitat or avifauna for the river system, although Binford (1989) describes bird sightings in the area. Lastly, one individual in this study wintered in the Bahía de Jiquilisco, Usulután, El Salvador (Fig. 3B). This bay is 63,500 ha and is designated as a national conservation area. Further, it includes the Xirihualtique-Jiquilisco Biosphere Reserve within its boundaries and is also a Ramsar site.

Capture and Transmitters

In Texas, adult Reddish Egrets ($n = 30$) were trapped in late May-June during the 2010-2012 and 2014 breeding seasons. Reddish Egrets (hereafter, egrets) were trapped on nine colonies using noose mats (Sutherland *et al.* 2004; McGowan and Simons 2005) placed within 1 m of the nest. Specific colonies and nests were chosen based on the number of other birds nesting on the island, location of the nest in relation to other species, and accessibility of the nest to minimize disturbance to other nesting birds. Egrets were trapped during mid to late incubation to minimize nest abandonment. In Florida, three adult egrets and one immature egret were trapped during the nonbreeding seasons (October-February) of 2009-2010 and 2013-2014, and one adult was captured during the breeding season (July) of 2010. Egrets were captured at foraging areas using a flip trap (Herring *et al.* 2008) or CO₂-powered net launcher (Advanced Weapons Technology). We recorded mass (g), tarsus length (mm), middle toe length (mm), culmen length (mm), and color morph, and affixed an aluminum leg band and a colored, alphanumeric plastic leg band to each egret. Solar GPS satellite platform terminal transmitters (PTT-100, Microwave Telemetry, Inc.) weighing 22 g were attached with Teflon ribbon

as a backpack harness. Satellite PTTs were < 3% of total body weight ($n = 26$) or 3.00-3.24% ($n = 9$) and were accurate to 18 m. Total handling time was < 30 min. The satellite PTTs were set to record locations six times per day, at 08:00, 09:00, 16:00, 17:00, 24:00, and 01:00 hr, coinciding with peak foraging times and nocturnal roosting. Two satellite PTTs placed on individuals in Florida recorded locations at 09:00, 10:00, 17:00, 18:00, 01:00, and 02:00 hr, two recorded locations at 05:00, 08:00, 10:00, 12:00, 14:00, 16:00, 18:00, and 21:00 hr and one recorded location at 09:00, 14:00, 16:00, 18:00, 20:00, and 22:00 hr. All times are in local time; Central Time for egrets marked in Texas and Eastern Time for egrets marked in Florida. Locations were downloaded once weekly from the Argos system (Argos 2011) and uploaded to Movebank (Wikelski and Kays 2016). We determined the sex of Reddish Egrets using blood samples ($n = 13$) and genetic samples from collected carcasses of marked individuals that died during the study period ($n = 7$), as blood samples had not been taken for those individuals. Discriminant analysis was used to determine sex of 15 egrets for which we did not have a DNA sample (Koczur *et al.* 2015).

Winter Season

In Texas, the winter season was October-February. Nest initiation dates have been recorded as late as mid-May to mid-June with re-nesting occurring as late as mid-July (McMurry 1971). Reddish Egrets incubate for ~26 days, and the time from hatching to fledging (without provisioning from adults) is ~9 weeks. Therefore, we assumed that Reddish Egrets ceased provisioning young by October. For each individual that migrated, the winter season began when it reached its wintering area and ended when it left the area. Colony formation in the Laguna Madre begins as early as March (Paul 1991); therefore, the winter season ended in February for resident egrets. In Florida, the winter season was determined for each individual because breeding can occur throughout the year (Paul 1991). GPS locations were used to determine that Reddish Egrets were no longer exhibiting nesting or provisioning behavior, as they no longer returned to the colony. Data were used until 25 February 2016 (Texas) and 12 November 2015 (Florida).

Nocturnal roosting locations were those recorded at 24:00 and 01:00 hr in Texas and 01:00, 02:00, 04:00, 05:00, and 21:00 hr in Florida (dependent on the duty cycle of the transmitter). An individual was considered roosting if the distance between the successive locations within a night was < 50 m, which takes into account the accuracy of the PTTs (± 18 m). If an egret moved > 50 m between the two locations, it was likely flying and those locations were excluded from roost site analyses.

Roosting and Foraging Habitat

The distance from roosting locations and foraging locations to the mainland or barrier island was measured in ArcMAP (Environmental Systems Research Institute 2015) using the near tool, and the mean (\pm SD) and least square mean (LSM) are reported. Benthic

habitat at roosting and foraging locations in the Laguna Madre, Texas, were delineated using a benthic habitat dataset (National Oceanic and Atmospheric Administration 2007). Habitat types included land (areas above high-tide line), unconsolidated sediment (< 10% seagrass coverage; unvegetated tidal flats), patchy seagrass (10-75% coverage), continuous seagrass (76-100% coverage), reef, emergent marsh, mangrove, and unknown (areas that could not be classified) (Finkbeiner *et al.* 2009). A land cover dataset and a benthic habitat dataset (National Oceanic and Atmospheric Administration 2007) were used to delineate habitat at sites in Florida. Habitat types included tidal flats, salt marsh, mangrove, oyster beds, coral, hard bottom, hardwood forest, and seagrass. The intersect tool in ArcMap was used to extract habitat features at each location. We created convex hulls in ArcMAP using the minimum bounding geometry tool and winter locations for each individual to delineate available area. Continuous seagrass and patchy seagrass habitat types were combined because of small sample sizes within these categories and because of the relative similarity in their structure. Benthic habitat datasets were not available for sites in Mexico and El Salvador; therefore, Google Earth (Google, Inc.) imagery was used to describe the roosting and foraging habitat of those sites. We used the package *adehabitatHS* v. 0.3.12 (Calenge 2011) in statistical program R (R Development Core Team 2014) to calculate Manly selection ratios (w_i ; Manly *et al.* 2007). We used the Design III model, which measures both habitat availability and use of habitat by each individual.

To further assess whether foraging and roosting habitat were similar, we used the *kerneloverlap* function in the *adehabitatHR* package (Calenge 2015) in statistical program R (R Development Core Team 2014), which quantified the degree of overlap between roosting areas and foraging areas (i.e., home ranges) in each winter season. Bhattacharyya's Affinity Index (BAI) was used to measure overlap and provided a value ranging from 0-1; a value of zero indicated no overlap, whereas a value of one indicated complete overlap (Bhattacharyya 1943; Fieberg and Kochanny 2005).

Distances Flown

Straight-line distances between successive locations were calculated using the Pythagorean Theorem in Microsoft Excel Office 2013 (Microsoft Corporation). We calculated the mean and standard error (SE) of distances moved from roost sites to morning foraging sites, from morning to evening foraging sites, and from evening foraging sites to roost sites for each individual. Three egrets from Florida had transmitters with different duty cycles, so times were matched as closely as possible to make analyses comparable. Because of a limited number of marked individuals at some sites (i.e., one egret in Campeche, Mexico), we grouped winter sites into regions: Texas, Tamaulipas, and Campeche were grouped as "Gulf Coast", and Oaxaca and Usulután were grouped as "Pacific Coast". Because of the marked differences in habitats available from other regions, Florida was not grouped with oth-

er sites and was treated as a distinct region. We used a three-way analysis of variance in SAS (SAS Institute, Inc. 2008; Proc MIXED) with time of day as a repeated measure to determine if time of day, gender, migratory status, region, and their interactions influenced mean distance moved. Years were pooled for analyses and the Shapiro-Wilk test was used to assess distribution of variances for each treatment combination.

Site Fidelity and Home Range

We assessed roost site and foraging site fidelity by calculating the area (ha) of 95% utilization distributions using the *adehabitatHR* package (Calenge 2015) in program R (R Development Core Team 2014). We then used Bhattacharyya's Affinity Index to measure the overlap of utilization distributions across successive and nonsuccessive winters. The averages of least square means for roosting fidelity and foraging fidelity were calculated. We used the least square cross validation method and all locations within a season for each individual. This metric was used to assess whether there were significant differences in areas of use among individuals. Analysis of variance in SAS (Proc GLM) was used to determine if home range size varied among sexes, color morphs, migratory status, or winter sites (grouped as above). The Shapiro-Wilk test was used to assess distribution of variances for each treatment combination.

RESULTS

Wintering Areas

Sixteen of the marked Reddish Egrets were resident in the Laguna Madre of Texas, USA, and 11 wintered at sites in Mexico and El Salvador. Two of the 16 residents made northward movements out of Laguna Madre during one winter, but not in subsequent winters; one female flew ~190 km from Laguna Madre to Galveston Bay (29° 32' 0" N, 94° 46' 0" W) for approximately 3.5 months and another moved ~100 km north of Laguna Madre into Aransas Bay (28° 2' 33" N, 96° 59' 37.72" W) for ~2 months. The other 14 resident egrets in Texas remained within the Laguna Madre through the duration of the study. Four Reddish Egrets dispersed to winter sites in Tamaulipas, Mexico. Three of the four egrets that wintered in Tamaulipas occurred just south of the border (≤ 32 km) within the Rio Grande Delta (Fig. 1A). The fourth was slightly farther inland within the northern Laguna Madre de Tamaulipas (~20 km

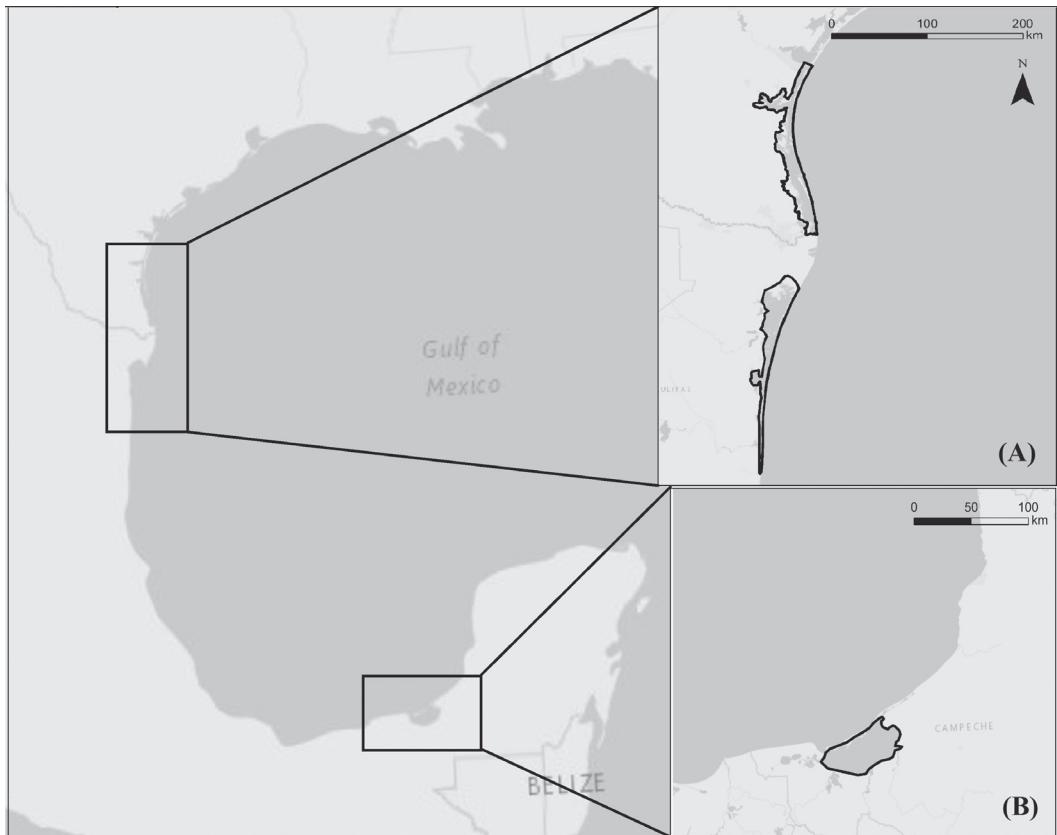


Figure 1. Winter sites (2010-2016) of adult Reddish Egrets marked with satellite transmitters in the Laguna Madre, Texas, USA, during the breeding season: (A) the Laguna Madre of Texas, USA, to the north and the Laguna Madre de Tamaulipas, Mexico, to the south and (B) the Laguna de Términos, Campeche, Mexico.

from the coastline). One egret wintered in the Laguna de Términos, Campeche, Mexico (Fig. 1B), and four egrets wintered in the Laguna del Mar Muerto, Oaxaca, Mexico (Fig. 3A). One egret wintered in Usulután, El Salvador, within a relatively small range in the Bahía de Jiquilisco (Fig. 3B). One egret wintered in the Bahía de Jiquilisco (Fig. 3B). One egret wintered in Usulután, El Salvador, within a relatively small range in the Bahía de Jiquilisco (Fig. 3B). One egret died during autumn migration west of Tampico, Mexico, prior to reaching its wintering area. Three egrets either died or the transmitter failed before their first winter season. The five egrets that were monitored in Florida remained resident and showed no migratory movements.

Roosting and Foraging Habitat

Roost locations of adult Reddish Egrets during winter occurred from 0.12 (0.10) to 3.20 (2.29) km from the mainland (overall

LSM = $1.37 + 0.71$ km) and distances were relatively consistent among sites. Benthic habitat at roost sites was assessed for 15 egrets that wintered within the Laguna Madre, Texas, totaling 2,746 locations. Nearly half (47.5%) of roost locations occurred on unconsolidated sediment, whereas ~22% of locations were in areas dominated by seagrasses (Fig. 4). Most egrets used unconsolidated sediment for roosting, which was more than expected ($w_i = 2.44$, SE = 0.31), whereas land ($w_i = 0.77$, SE = 0.32) and seagrass ($w_i = 0.45$, SE = 0.05) were used slightly less than expected. A total of 917 locations were used to examine benthic habitat at roost sites for five egrets wintering in Florida. Salt marsh ($w_i = 5.64$, SE = 2.57) was used more than expected, whereas tidal flats ($w_i = 0.88$, SE = 0.21) and seagrass ($w_i = 0.76$, SE = 0.45) were used slightly less than expected. However, habitats used varied among individuals (Fig. 5).

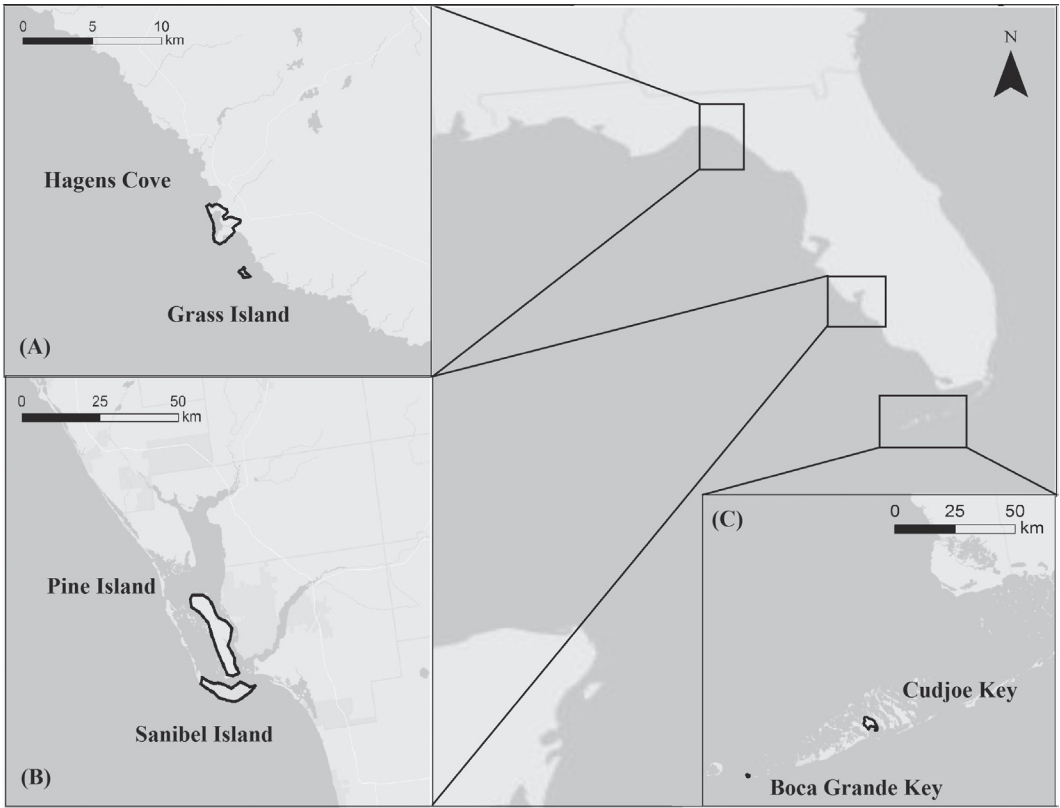


Figure 2. Winter sites on (A) the upper coast of Florida, USA (2014-2015), (B) the central coast of Florida, USA (2014-2015), and (C) the Florida Keys, USA (2010-2011) for Reddish Egrets marked with satellite transmitters.

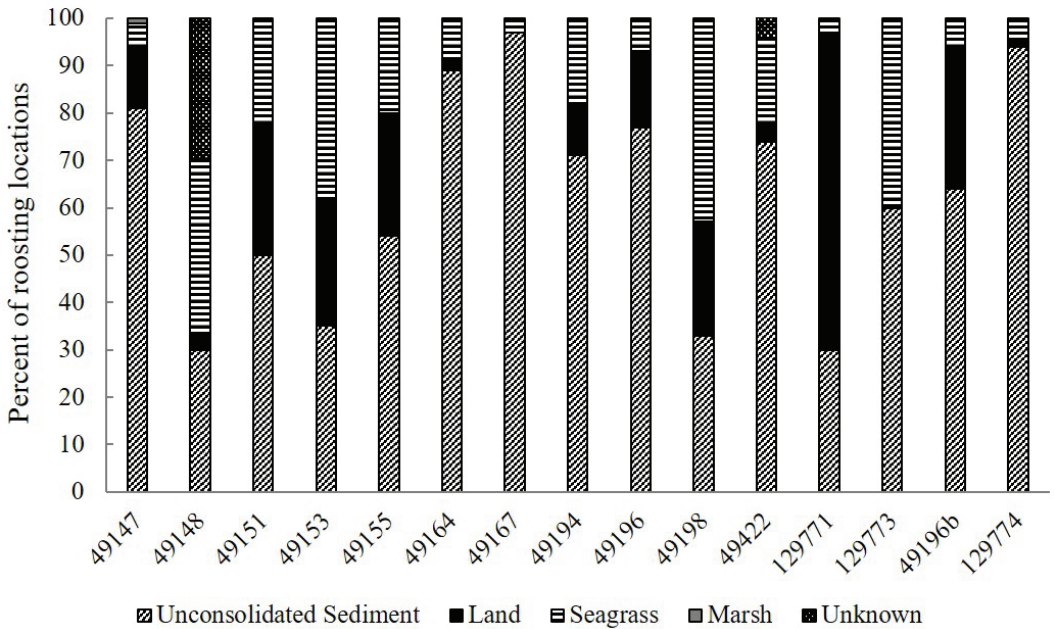


Figure 3. Winter sites of adult Reddish Egrets marked with satellite transmitters in the Laguna Madre, Texas, USA during the breeding season: (A) the Rio Verde, Oaxaca, Mexico, to the west and the Laguna Mar Muerto, Oaxaca and Chiapas, Mexico, to the east (2010-2016) and (B) the Bahía de Jiquilisco, Usulután, El Salvador (2014-2016).

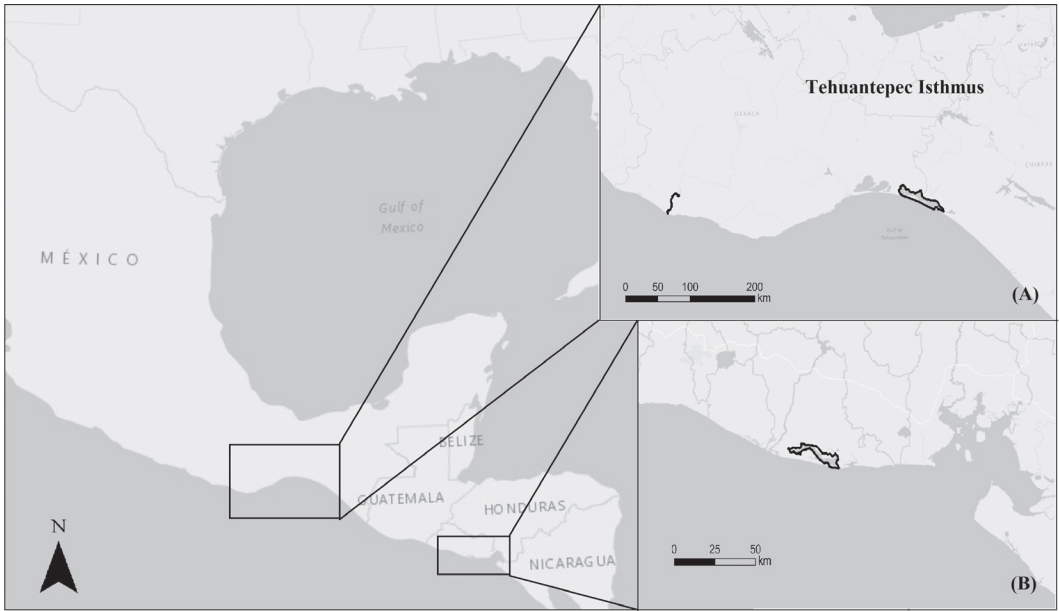


Figure 4. Percent of roosting locations at benthic habitat types for 15 Reddish Egrets wintering in the Laguna Madre, Texas, USA, during 2010-2016.

The mean distance from foraging locations to the mainland/barrier island ranged from 0.04 to 3.82 km among individuals, and the LSMs for each winter area ranged from

0.04 km in Campeche to 2.04 km in Texas. The overall LSM was 1.71 km. Benthic habitat was assessed at foraging sites for 15 egrets that wintered in the Laguna Madre, Texas,

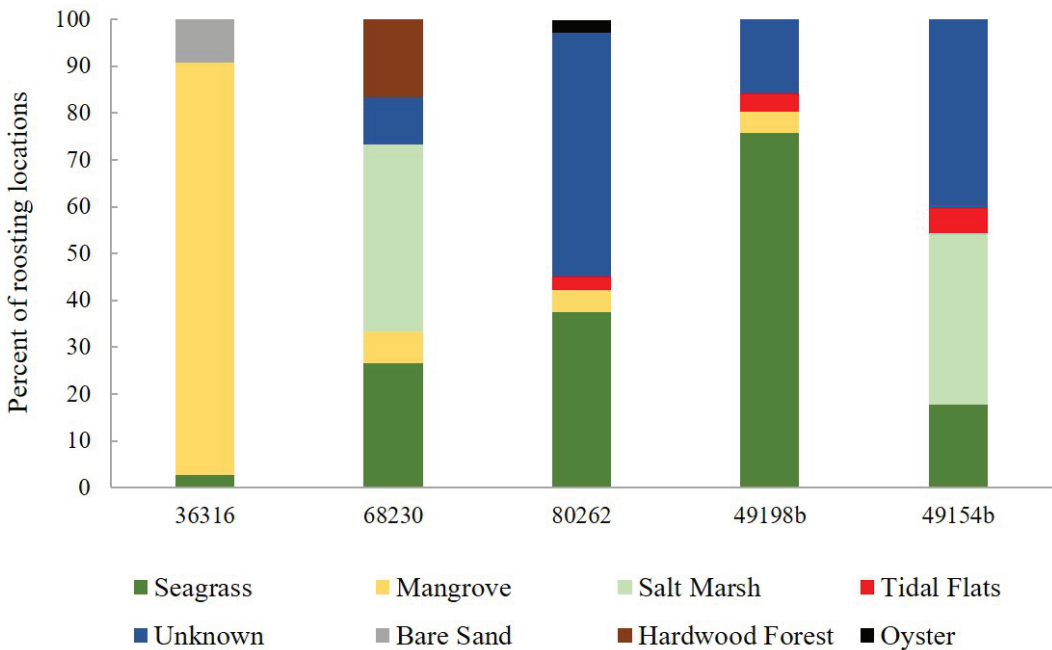


Figure 5. Percent of roosting locations at benthic habitat types of five Reddish Egrets wintering in Florida, USA, during 2010-2015.

totaling 12,784 foraging locations. Similar to roosting habitat, Reddish Egrets in Texas showed preference for unconsolidated sediment ($w_i = 2.71$, $SE = 0.45$) and avoided foraging areas with seagrass ($w_i = 0.25$, $SE = 0.07$). Sixty-three percent of foraging locations in Texas were on unconsolidated sediment, whereas ~13% were in areas dominated by seagrass (Fig. 6). Benthic habitat was assessed for five egrets that wintered in Florida using 4,706 foraging locations. Similar to Texas, Reddish Egrets in Florida showed a tendency to avoid foraging in areas dominated by seagrass ($w_i = 0.44$, $SE = 0.04$). Egrets in Florida showed preference for tidal flats ($w_i = 7.96$, $SE = 1.51$) and salt marsh ($w_i = 2.08$, $SE = 0.96$), yet habitat use varied considerably among individuals (Fig. 7).

Sixty-six percent of Reddish Egrets showed considerable overlap ($BAI > 0.50$) of foraging and roosting areas during each winter (Table 1). Forty-seven percent of the 58 individual*year combinations exhibited nearly complete overlap ($BAI > 0.97$). Egret 49148 was a resident in Texas and had no overlap of foraging and roosting areas in the first winter, and a low degree of overlap in subsequent winters. This egret primarily foraged along a chain of islands in the Laguna

Madre. It roosted ~3 km north in shallow water and on a small island, and on a cabin in the middle of the water ~0.5 km west of foraging sites. Egret 49422b wintered in Tamaulipas, adjacent to what appears to be abandoned salt or aquaculture ponds. Foraging and roosting areas overlapped (Table 1); however, there were distinct roost sites that occurred in the center of a tidal flat and shallow water of a wetland. In Campeche, Mexico, egret 49154 exhibited extensive overlap in foraging and roosting areas in an estuary surrounded by mangroves near an inlet (Table 1). In Florida, all egrets exhibited overlap between foraging and roosting areas; however, egret 49154b exhibited the smallest degree of overlap (Table 1). This egret foraged around Hagens Cove and roosted approximately 3.5 km south on Big Grass Island (Fig. 2A). All roost locations were on this island, and some foraging locations occurred near the island.

Distances Flown

The mean straight-line distance between roosting and morning foraging locations, morning and afternoon foraging locations, and afternoon foraging and roosting loca-

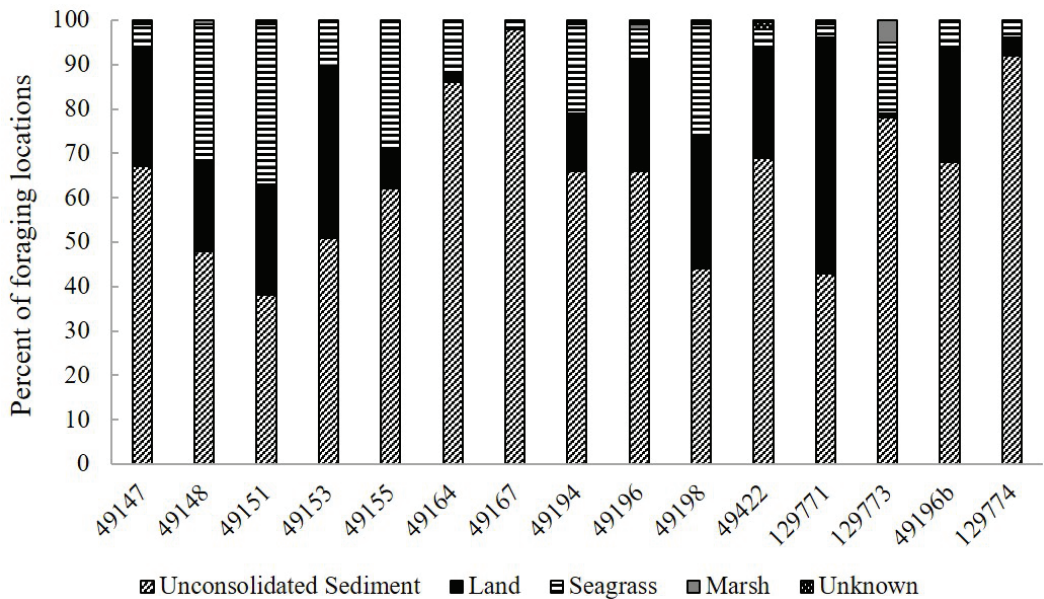


Figure 6. Percent of foraging locations at benthic habitat types for 15 Reddish Egrets wintering in the Laguna Madre, Texas, USA, during 2010-2016.

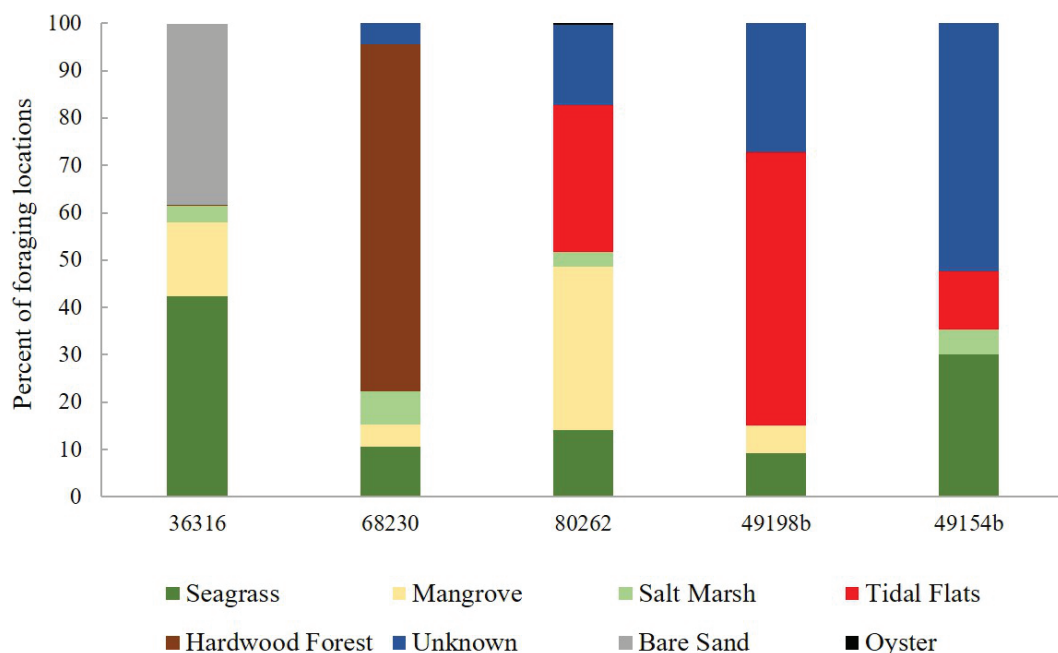


Figure 7. Percent of foraging locations at benthic habitat types of five Reddish Egrets wintering in Florida, USA, during 2010-2015.

tions ranged from 0.1 to 4.8 km across all birds. The main effects of migratory status ($F_{22} = 27.22$, $P < 0.001$) and location ($F_{48} = 27.94$, $P < 0.001$) were significant. Reddish Egrets that were resident flew greater distances between foraging and roosting areas (2.28 km, SE = 0.15) than individuals that were migratory (0.99 km, SE = 0.18). Also, egrets wintering in Florida flew shorter distances (0.41 km, SE = 0.24) on average than egrets wintering on the western Gulf (2.27 km, SE = 0.12) and Pacific Coasts (2.23 km, SE = 0.25). There was a significant interaction between sex and time of day ($F_{48} = 3.63$, $P = 0.034$). Overall, females flew greater distances than males between the morning and evening foraging locations (1.70 ± 0.21 vs. 1.08 ± 0.17 km), whereas distances from the roost to morning foraging locations (2.28 ± 0.21 vs. 1.88 ± 0.17 km) and from evening foraging to roost locations (1.37 ± 0.21 vs. 1.49 ± 0.17 km) were similar. Overall, the LSM distance between successive daily roosting locations was $2.93 (\pm 2.61)$ km and ranged from 0.10 (± 0.13) to 8.62 (± 15.61) km among individuals and across all winters. The median distance ranged from 0.01 (± 0.01) to 3.46 (± 3.34) km.

Fidelity

Reddish Egrets exhibited a high degree of fidelity to roosting areas between successive years. Eighteen of the transmitters were active for 2 or more years and were therefore used to assess site fidelity across years. All individuals exhibited some degree of overlap in roosting areas, with 79% of 28 possible individual*year combinations having $\geq 50\%$ overlap (Table 2). The average least square mean BAI was 0.65 for roosting areas and 0.71 for foraging areas across all individuals. Egret 49164 had very low overlap between the first two years; it flew to Galveston Bay (188 km) during one wintering period, but did not make the same trip in subsequent winters. Reddish Egrets also exhibited relatively high fidelity to foraging areas across successive years; 82% of 28 individual*year combinations had $\geq 50\%$ overlap (Table 2). The average least square mean BAI was 0.71 for foraging areas across all individuals. Four of five egrets had $\geq 45\%$ overlap across all nonsuccessive winters (Table 3). Egret 49164 had low overlap in nonsuccessive winters that included the winter in which it moved to Galveston Bay.

Table 1. Bhattacharyya's Affinity Index of Reddish Egret foraging and roosting area overlap in each winter (Year 1 = winter of 2010-2011, Year 2 = winter of 2011-2012, etc.; bold text indicates where the individual occurred for the majority of the winter).

Bird ID	Winter Site	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
49154	Campeche, Mexico	0.72	0.69	0.79			
129772	Usulután, El Salvador					0.59	0.48
49198	Florida, USA	0.27	0.50				
49154b	Florida, USA	0.12	0.15				
36316	Florida, USA	0.40	0.26				
80262	Florida, USA	0.28	0.88				
68230	Florida, USA	0.50					
49150	Oaxaca, Mexico	0.99	0.99	0.99			
49156	Oaxaca, Mexico	0.99					
49166b	Oaxaca, Mexico					0.99	0.76
49195	Oaxaca, Mexico		0.99	0.99	0.99		
49149	Tamaulipas, Mexico	0.59					
49422b	Tamaulipas, Mexico			0.34	0.60		
49147	Texas, USA	0.98					
49147b	Texas, USA		0.99				
49148	Texas, USA	0.00	0.16	0.13	0.14		
49151	Texas, USA		0.98				
49153	Texas, USA		0.41	0.3	0.29	0.30	
49155	Texas, USA		0.99				
49164	Texas, USA		0.99	0.98	0.98	0.99	0.99
49167	Texas, USA		0.55				
49194	Texas, USA	1.00	0.99				
49196	Texas, USA		0.99				
49196b	Texas, USA					0.99	1.00
49198	Texas, USA		0.98				
49422	Texas, USA	0.26	0.98				
129771	Texas, USA					0.82	0.88
129773	Texas, USA					0.32	
49165	Texas, USA / Tamaulipas, Mexico	0.97	0.98				
129774	Texas, USA / Tamaulipas, Mexico					0.99	

Home Range Size

Year was not a significant variable explaining variation in home range size; therefore, home range areas were averaged across years. An ANOVA was used to assess variation between sexes, morphs, migratory status, and winter locations. Treatment combinations were not normally distributed, so the natural logarithm of home range size was used. There was a significant interaction between sex and location ($F_{2,24} = 7.23$, $P = 0.004$). Males and females had similar average home range areas in Florida (39 ha, 95% CI = 7-224 vs. 75 ha, 95% CI = 9-639, $P = 0.659$) and at Pacific Coast sites (1,920 ha, 95% CI = 334-10,938 vs. 1,636 ha, 95% CI = 194-13,905, $P = 0.943$). At western Gulf Coast sites, males had a considerably smaller

average home range area than females (116 ha, 95% CI = 40-337 vs. 11,849 ha, 95% CI = 4,946-28,282; $P < 0.001$).

DISCUSSION

This was the first study to examine the winter ecology of Reddish Egrets in various portions of their range, and the results contribute to the limited knowledge base on this rare species. Resident egrets in Texas and Florida did not make any large movements during winter months. Migratory individuals from the Texas breeding population wintered in several Mexican States and in El Salvador. Reddish Egrets used benthic habitat differently throughout the range, and also exhibited individual variation in habitat use. The

Table 2. Overlap of Reddish Egret roosting areas (outside parentheses) and foraging areas (in parentheses) across successive winters using Bhattacharyya's Affinity Index. (Winter 1 = winter of 2010-2011, Winter 2 = winter of 2011-2012, etc.).

Bird ID	Sex	Migratory	Winter 1-2	Winter 2-3	Winter 3-4	Winter 4-5	Winter 5-6
49148	M	N	0.58 (0.96)	1.00 (0.96)	0.93 (0.96)		
49150	M	Y	0.97 (0.96)	0.93 (0.92)			
49153	M	N		0.65 (0.47)	0.93 (0.83)	0.94 (0.82)	
49154	M	Y	0.61 (0.60)	0.99 (0.91)			
49164	F	N		0.07 (0.08)	0.88 (0.90)	0.91 (0.93)	0.82 (0.84)
49165	F	Y	0.22 (0.27)				
49194	F	N	0.63 (0.65)				
49195	M	Y		0.90 (0.88)	0.96 (0.94)		
49422	M	N	0.09 (0.11)				
49422b	M	Y			0.76 (0.88)		
49166b	F	Y					0.30 (0.50)
49196b	F	N					0.70 (0.72)
129771	F	N					0.92 (0.91)
129772	M	Y					0.92 (0.84)
36316	M	N	0.88 (0.28)				
49154b	M	N					0.87 (0.90)
49198b	M	N					0.11 (0.93)
80262	F	N					0.19 (0.80)

Reddish Egret Conservation Action Plan states that roosting habitat is indistinguishable from foraging habitat (Wilson *et al.* 2014). These results provide evidence to support this conclusion for egrets wintering in Texas. Thus, on wintering areas, the conservation of foraging habitat alone should meet the requirements during that time of year.

Table 3. Roost area overlap and foraging area overlap of Reddish Egrets across nonsuccessive winters using Bhattacharyya's Affinity Index (BAI). (Winter 1 = winter of 2010-2011, Winter 2 = winter of 2011-2012, etc.).

ID	Roost		Forage	
	Winter	BA	Winter	BAI
49148	1 to 3	0.54	1 to 3	0.90
	1 to 4	0.65	1 to 4	0.97
	2 to 4	0.94	2 to 4	0.98
49150	1 to 3	0.84	1 to 3	0.81
	2 to 4	0.6	2 to 4	0.68
	2 to 5	0.51	2 to 5	0.45
49153	3 to 5	0.98	3 to 5	0.96
	1 to 3	0.64	1 to 3	0.73
	2 to 4	0.11	2 to 4	0.12
49164	2 to 5	0.08	2 to 5	0.08
	2 to 6	0.13	2 to 6	0.14
	3 to 5	0.96	3 to 5	0.96
	3 to 6	0.81	3 to 6	0.79
	4 to 6	0.97	4 to 6	0.96
	2 to 4	0.90	2 to 4	0.88
	49195	2 to 4	0.90	2 to 4

Both roosting and foraging locations were an average of ~2.5 km from the mainland or barrier island. The distance that foraging and roosting sites are from the mainland, and the use of foraging and roost sites in general, may depend on a number of factors, including the extent of the lagoon system, water depth, prey distribution, and vulnerability to predators and human disturbance. This has been observed in other avian species. For example, Krapu *et al.* (1984) found that Sandhill Cranes (*Antigone canadensis*) on the Platte River, Nebraska, USA, selected roost sites where the river channel was ≥ 150 m wide, presumably because the water barrier provided safety from predators. The effect of human disturbance on roosting California Brown Pelicans (*Pelecanus occidentalis californicus*) was also documented; disturbance led to a 21% decrease in roost site use (Wright *et al.* 2007).

Unconsolidated sediment, such as shallow wind tidal flats, was the primary benthic habitat type used for both roosting and foraging. The foraging habitat of Reddish Egrets is described as open flats with little vegetation (Lowther and Paul 2002). Bates *et al.* (2016) found that most Reddish Egrets in the Laguna Madre, Texas, foraged in ar-

areas with $\leq 10\%$ seagrass coverage. Our results support those of Bates *et al.* (2016), as seagrass was used less than expected based on availability for foraging; however, some egrets used seagrass more than expected for roosting. Benthic habitat data sets were not available for Mexico or El Salvador; therefore, habitat selection at these sites was not quantified. Habitat use clearly depends on the availability of habitat types, which differs across a species' range. For example, in the Laguna Madre of Texas mangrove comprises a very small area, whereas in Florida mangrove habitat is more prevalent and may be more important for Reddish Egrets there, as they used this habitat type for both roosting and foraging. Temporal availability of foraging and roosting habitats for Reddish Egrets is influenced by changes in water depth as a result of tidal fluctuations (Bates *et al.* 2016; Calle *et al.* 2016). Reddish Egrets have an affinity for shallow water for foraging, and small changes in water level can result in large changes in availability of habitats (Bates *et al.* 2016). Future research of habitat use should attempt to examine the relationship between the availability of benthic habitat and fluctuations in water level.

Studies of flight distances have largely focused on the distances birds fly from the nest site to foraging sites (Maccarone *et al.* 2012; Brzorad *et al.* 2015), and waterbird flight distances during the nonbreeding season are not as well studied. As with breeding colonies, high quality roost sites should be in close proximity to foraging areas, thereby reducing the energy expenditure a bird incurs by flying between sites (Rogers 2003; Rogers *et al.* 2006). This would seem particularly important for active foragers such as Reddish Egrets that expend considerable energy while foraging (Bates and Ballard 2014). If roosting habitat and foraging habitat are similar, relatively short flight distances would be expected, which is consistent with our results. On average, Reddish Egrets flew approximately 2 km between foraging and roosting sites during winter. Similar results have been observed in Wood Storks (*Mycteria americana*) wintering in Georgia, USA, which foraged within 2 km of roosts (Bryan

et al. 2002). Also, Black Storks (*Ciconia nigra*) wintering in Africa generally roosted within 3 km of foraging areas (Chevallier *et al.* 2010). Based on our results, it appears that Reddish Egrets can be quite plastic in their use of habitats for roosting, and the habitat used depends on its availability within the individual's range.

Reddish Egrets in Florida flew shorter distances between foraging and roosting areas than egrets in the other locations. Observations of Reddish Egrets in Florida suggest that they are highly territorial at foraging areas (G. Kent, unpubl. data). This may be a result of limited foraging habitat in the region, the spatial and temporal distribution of prey, abundance of prey, or the density of competitors (Goldberg *et al.* 2001; Maccarone and Brzorad 2007). There is no evidence of foraging territoriality for Reddish Egrets in Texas; they have been observed foraging both solitarily and in groups (Bates and Ballard 2014). Reddish Egrets that remained resident in Texas flew relatively longer distances between foraging and roosting areas compared to egrets that migrated. The Laguna Madre exhibits semi-annual changes in water depth, with high tides typically in May and October and low tides in February and July (Tunnell and Judd 2002). Variation in water depth is primarily a result of wind speed and direction, which can influence water levels quickly and subsequently influence the availability of foraging habitat. Bates *et al.* (2016) found that available foraging habitat in the Laguna Madre decreases during winter months. This may lead to egrets in Texas flying farther distances between productive foraging areas or changing roosting locations in response to prey movement.

Recent research has shown that many avian species exhibit high winter site fidelity (Noel and Chandler 2007; Clark *et al.* 2016). Overall, we found Reddish Egrets to exhibit a relatively high degree of site fidelity to both roosting and foraging areas. Home range size varied considerably among individuals in this study. Home range sizes were largest in Texas and smaller at all other locations. Home range size also could be influenced by the area of the system, the degree of territo-

riality, the spatial and temporal availability of foraging habitat, and/or the availability prey species (Bautista *et al.* 2017).

Our results show that the Reddish Egret uses habitat differently throughout its range, which can be used to direct management decisions for habitat conservation. The Reddish Egrets in this study also exhibited fidelity to winter sites, with some individuals occupying a small area throughout winter. For species that show strong fidelity to sites, populations may be more susceptible to habitat loss and disturbance (Mittelhauser *et al.* 2012). Due to their habitat specialization, Reddish Egrets are particularly susceptible to habitat loss. Lastly, migratory individuals wintered in Tamaulipas, Oaxaca, Chiapas, and Campeche, Mexico, which support resident populations of Reddish Egrets (Paul 1991). Although Paul (1991) reported that Reddish Egrets are not known to breed in El Salvador, information is lacking for that area (Wilson *et al.* 2014) and other ardeids are known to breed in the Bahía de Jiquilisco, Usulután, El Salvador. The decrease in available foraging habitat within the Laguna Madre, Texas, during winter is believed to be a limiting factor for the winter population of Reddish Egrets in Texas (Koczur 2017), providing further support for the necessity to conserve foraging sites for this habitat specialist.

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